

**EVALUATION OF THE ZOOPLANKTON COMMUNITY
OF LIVINGSTON RESERVOIR, TEXAS,
AS RELATED TO PADDLEFISH FOOD RESOURCES**

A Thesis

by

CASEY KENNETH MOORE

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

December 1993

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ABSTRACT

Evaluation of the Zooplankton Community of Livingston Reservoir, Texas,
as Related to Paddlefish Food Resources. (December 1993)

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Paddlefish, *Polyodon spathula*, are large freshwater fish that once were numerous throughout the Mississippi River and Gulf Slope drainages of the United States, but they have experienced a decline in the twentieth century. After paddlefish were declared endangered in Texas in 1977, a restoration program was begun that included stocking young fish in and upstream from Livingston Reservoir, Texas.

The zooplankton community of Livingston Reservoir was examined in terms of composition, abundance, distribution, and organisms appropriate as food resources for paddlefish. By comparing the range of interraker distances of paddlefish (0.06-0.08 mm) to size measurements of different zooplankton taxa, it was determined that paddlefish do not utilize small rotifers and copepod nauplii as efficiently as they do larger copepods and cladocerans. Overall zooplankton abundances were greater than those reported for other Texas reservoirs, but the community was dominated in terms of abundance and biomass by small rotifers and copepod nauplii. All taxa (rotifers, cladocerans, and copepods) were comprised of relatively small organisms.

Zooplankton were distributed unevenly along the length of the reservoir, with highest abundances in the mid-portions and lower abundances near the

Trinity River inflow and Livingston dam. Zooplankton were evenly distributed among the openwater and backwater stations. Cladocerans and copepods exhibited strong diel vertical migrations.

A bioenergetics model was developed to predict the paddlefish biomass that could be supported in Livingston Reservoir, and predicted a density of 1.17 kg/ha, and a range of best estimates of 0.06 to 10.45 kg/ha. The predicted densities, which might be a result of the relatively small size structure of the zooplankton community, are lower than the targets of the restoration plan, and suggest that present goals for paddlefish in Livingston Reservoir might need to be revised.

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INTRODUCTION AND REVIEW OF THE LITERATURE

The paddlefish, *Polyodon spathula*, is the only species of the family Polyodontidae found in North America, and is one of the largest freshwater fishes (Russell 1986). It can grow to more than six feet in length and weigh over one hundred pounds. It is distinguished physically by a large rostrum which is generally between one-third and one-fourth of the total body length (Stockard 1907). Paddlefish found in lakes and reservoirs are more heavily proportioned than the more slender and "shark-like" paddlefish in rivers (Stockard 1907). Female paddlefish are generally larger and heavier than males, due to their large ovaries and the presence of many eggs (Stockard 1907; Rosen et al. 1982; Pitman 1991).

Historically, paddlefish were found in the lakes, rivers, and large streams of the Mississippi Valley, the Gulf Slope drainages, and the Great Lakes (Gengerke 1986). Although detailed records of abundance of the species have never been compiled, it appears that paddlefish began to experience a decline in the early 1900's as the worldwide demand for paddlefish roe and flesh increased (Pasch and Alexander 1986). The decline of the species has continued in recent decades as navigation, siltation, and industry have reduced the amount of habitat suitable for paddlefish populations (Southall and Hubert 1984; Sparrowe 1986). The primary factor leading to the decline seems to be impoundment of rivers, which disrupts paddlefish spawning habits (Unkenholz 1986). The impact of impoundment has been apparent in several Texas river systems in

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which dams have been constructed. In these systems an increased abundance of paddlefish downstream from the dam and the elimination of paddlefish upstream from the dam followed soon after impoundment (Unkenholz 1986).

Out of 26 states that contained paddlefish populations historically, 16 still have active paddlefish fishing (Gengerke 1986). Paddlefish are protected in 6 states, but have been extirpated in New York, Pennsylvania, Maryland, and North Carolina (Gengerke 1986) (Figure 1).

Although there is little historical data to confirm the abundance of paddlefish in Texas, there are records of their occurrence in several eastern Texas river systems (Pitman 1991). Reports indicate that the occurrence of paddlefish in Texas has decreased throughout the twentieth century (Combs 1986; Sparrowe 1986). This decline stimulated the Texas Parks and Wildlife Department (TPWD) to examine the abundance of paddlefish and their habitat in Texas. They concluded that "Reservoir construction, timber harvest techniques, pollution, urbanization, and industrialization have so modified stream characteristics in East Texas that [the paddlefish] is only occasionally observed" (Pitman 1991). In 1977, TPWD declared the species endangered in Texas, and made retention of the fish and export of products derived from Texas paddlefish illegal (Pitman 1991).

TPWD began efforts to restore the species to Texas in 1987 (Pitman 1991). These efforts included restoration programs and cooperative research with state universities and state agencies. The Texas Paddlefish Recovery Plan was completed in 1991, and included a 10-year program of stocking paddlefish in five eastern Texas river systems beginning in 1989 (Pitman 1991).

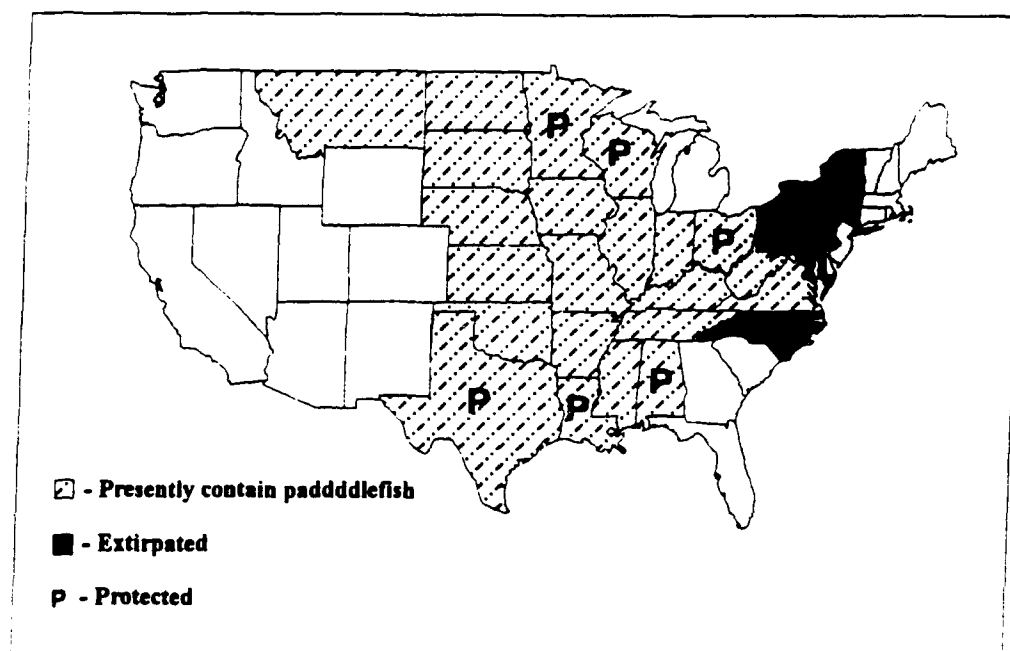


Figure 1. Status of paddlefish in the United States and states that contain them (modified from Pitman 1991).

As part of this plan, 162,012 paddlefish fingerlings have so far been stocked in and upstream from Livingston Reservoir in the Trinity River system. The Trinity River, which begins near Dallas and flows 885 km into Trinity Bay near Houston, is considered one of the most suitable systems for paddlefish populations because it contains appropriate paddlefish spawning habitat (Pitman 1991).

Paddlefish are zooplanktivorous filter feeders and tend to inhabit slow-moving, zooplankton-rich areas in the summer (Southall and Hubert 1984). Paddlefish move into faster-moving waters in the spring to seek out spawning grounds (Southall and Hubert 1984). They head upstream, seeking out gravel beds and increased flow, which are necessary for attachment and aeration of the eggs (Russell 1986).

Paddlefish Food Resources

Paddlefish exhibit two distinct types of feeding behaviors during their lifetime, depending on their stage of maturity. Post-larval and juvenile paddlefish are particulate feeders that actively select and pursue individual prey items (Ruelle and Hudson 1977; Mims and Schmittou 1989). As particulate feeders they must select relatively large prey that can be easily detected and pursued (Durbin 1979). Such food items include larger crustacean zooplankton (*Daphnia* sp., larger cyclopoid and calanoid copepods), aquatic insects, and terrestrial insects (Ruelle and Hudson 1977).

As paddlefish mature they begin to develop gill rakers, which are rows of fine filaments on the inside edge of the gill arch. The gill rakers are used to filter food items from the water, and are usually fully functional by the time the fish

reaches a total length of 120-350 millimeters (1-2 years) (Michaletz et al. 1982; Pitman 1991). Once the gill rakers have become functional, the paddlefish switches from particulate feeding to indiscriminate filter feeding, swimming with the mouth open, the gills flared, and using the gill rakers like a sieve to capture food items from the water.

Filter feeding allows adult paddlefish to capture smaller prey items and feed more efficiently than juvenile fish, since they do not have to expend energy to actively hunt and capture each individual food item (Durbin 1979). Therefore, the adults are able to utilize smaller zooplankton, which include smaller cladocerans and copepods, and even some rotifers (Rosen and Hales 1981). The minimum food size an adult fish is able to consume is limited only by the size of the gill rakers, or more precisely, by the size of the space between the gill rakers (the interraker distance) through which potential food items are able to pass.

Zooplankton

Zooplankton are a major portion of the primary-consumer trophic level within aquatic ecosystems. Because they feed upon the primary producers within the system (algae, bacteria, etc.) and are fed upon by larger organisms, including fish, they are an important link in aquatic system food webs.

The freshwater zooplankton community is comprised of a wide variety of organisms, including coelenterates, larval trematode worms, gastrotrichs, mites, protozoa, and larval insects, but is largely dominated by three major groups: rotifers, cladocerans, and copepods (Wetzel 1983).

1) Rotifers

Rotifers are pseudocoelomates that are generally unsegmented and

bilaterally symmetrical (Thorp and Covich 1991). Most rotifers are herbivorous, but some are parasitic, or predacious (Wallace and Snell 1991). Rotifers are found almost exclusively in freshwater: fewer than 5% of more than 2500 described species are found in marine habitats (Pennak 1989).

2) Cladocerans

Cladocerans are a diverse group of crustaceans that contains about 400 species (Dodson and Frey 1991). They share similar mouth parts and phyllopods, which are the leaf-like thoracic legs used for filter-feeding (Thorp and Covich 1991). Many cladocerans are not clearly segmented, and are covered by a bivalved shell or carapace (Pennak 1989). Cladocerans include both herbivores and predators and are found in a wide variety of habitats within the aquatic community.

3) Copepods

Copepods are a class of primarily free-living crustaceans distinguished by a cylindrical, segmented body, two posterior caudal rami, and a single anterior, simple eye (Thorp and Covich 1991). The free-living copepods comprise three major suborders: Calanoida, Cyclopoida, and Harpacticoida (Williamson 1991). Copepods are found in a wide variety of habitats within the aquatic community, and can be herbivorous, predacious, or omnivorous (Williamson 1991). The larval and juvenile stages of copepods, termed nauplii, often make up a large proportion of the zooplankton community within a given area.

Zooplankton Community Structure

The composition, seasonal abundance, and dynamics of a zooplankton community are complex. Each zooplankton community is influenced by a

number of biotic and abiotic variables, and will react differently to each of these variables according to local habitat. The composition of a zooplankton community depends upon a multitude of factors, including environmental factors, food type and availability, predation pressure, etc., and it is therefore impossible to describe any particular population without detailed study (Dodson and Frey 1991). Most zooplankton communities, though, include organisms from each of the three main zooplankton groups (rotifers, cladocerans, and copepods) that are distributed differently, and occur in different numbers, relative to each other within a body of water (Hutchinson 1967).

Rotifers usually are present in large quantities relative to the cladocerans and copepods, but due to their small size they do not make up the greatest proportion of the zooplankton community biomass (Williamson 1991). Some common rotifers in many lakes belong to the genera *Trichocerca*, *Synchaeta*, *Polyarthra*, *Asplancha*, *Keratella*, and *Brachionus* (Hutchinson 1967).

Rotifers generally are the most abundant type of zooplankton in terms of numbers of individuals. Rotifers commonly are found at densities of around 1000 organisms per liter, but have been found at much higher densities (Edmondson 1946), and have been reported as high as 100,000 organisms per liter (Wallace and Snell 1991). Edmondson (1946) found densities of single species approaching 100 organisms per liter.

Cladocerans usually are less abundant than rotifers, but often make up an important part of the community biomass due to their larger size. Some common genera include *Daphnia*, *Bosmina*, *Diaphanasoma*, and *Ceriodaphnia* (Pennak 1989).

Along with the cladocerans, copepods usually make up the greatest portion of zooplankton community biomass (Thorp and Covich 1991). Some common cyclopoid species include *Mesocyclops edax* and *Acanthocyclops vernalis* (Williamson 1991). Diaptomidae is the most common family of calanoid copepod in North America, and it is somewhat common to find more than one species of this family in a zooplankton community (Williamson 1991). Members of the order Harpacticoida are mainly benthic organisms and usually are not found among the plankton of a lake or reservoir (Williamson 1991). Members of the crustacean class Ostracoda are also usually found only in the benthos, and rarely in the water column (Delorme 1991).

Cladocerans and copepods generally are found in smaller numbers than rotifers, usually occurring at less than 100 organisms per liter (Dodson 1974; Pennak 1989). Repsys (1982) found densities of all crustacean zooplankton (cladocerans and copepods) less than 20 organisms per liter in the Missouri River, and Dodson (1974) found copepod densities between zero and 100 organisms per liter in small Colorado ponds. Local conditions, though, can lead to temporarily high densities of copepods, with numbers approaching 1000 per liter (Pennak 1989). Copepod nauplii densities have also been reported in the thousands per liter in areas of the Mississippi River Plume with high freshwater influence (Dagg 1991).

Zooplankton also show marked differences in seasonal abundances. Populations may be monocyclic (one population maximum during the year), dicyclic (two population maxima), acyclic (no pronounced maxima), or none of the above (Pennak 1989). The classic cycle for a zooplankton community shows

few organisms present during the winter, increasing abundances during the spring as the water warms and more food becomes available, and then decreasing abundances during the summer and fall (Pennak 1989). Cladocerans exhibit pronounced population pulses following algal blooms during the spring or fall (Pennak 1989).

The individual taxa of zooplankton exhibit distinct patterns of distribution, both horizontally and vertically, within a lake or reservoir. Such patterns vary widely among types of organisms and lakes, and even within individual lakes (Wallace and Snell 1991).

Types of zooplankton within a lake tend to be distributed differentially among the open pelagic zone and the shallower, calmer backwaters and littoral zones. Approximately 75% of rotifer species are littoral, although those that are found in open waters tend to be present in greater numbers than littoral species (Hutchinson 1967; Pennak 1989). Among copepods, cyclopoids are generally more littoral, while calanoids are more pelagic (Williamson 1991). There is a tendency for all types of zooplankton to include some genera and species that prefer either open waters or backwaters.

The differential distribution of zooplankton vertically in the water column has been well documented. In general, zooplankton tend to move down in the water column during the day in order to avoid predators, and move toward the surface at dusk and during the night in order to feed on the phytoplankton concentrated at the surface (Dodson 1990; Ohman 1990). Although rotifers do migrate vertically, the magnitude of the migration is usually only 1-2 meters (Magnien and Gilbert 1983). The magnitude of vertical migration in cladocerans

and copepods can be up to 10 meters, and reverse vertical migration has been shown in both (Dodson and Frey 1991; Williamson 1991).

Physiochemical Parameters

Physiochemical parameters may also play a large part in determining the suitability of an area for any fish population. The physical conditions of a reservoir or river, such as current, water temperature, etc., can influence whether paddlefish will successfully spawn and encounter suitable feeding areas. Chemical parameters, such as nitrate and ammonia levels, can influence the growth and development of young paddlefish and even the health of the whole population. Such physiochemical parameters indirectly affect paddlefish in a different, but significant, manner by influencing the existence, abundance, composition, and ultimate success of their zooplankton food source and the phytoplankton population upon which many of the zooplankton feed.

Objectives

The objectives of this study were:

- 1) To determine the appropriate zooplankton food resources of paddlefish in Livingston Reservoir, Texas.
- 2) To describe the seasonal composition, abundance, and distribution of the Livingston Reservoir zooplankton community, and relate this community to its suitability to support a paddlefish population.
- 3) To evaluate seasonal patterns of physiochemical parameters in Livingston Reservoir as related to environmental tolerance and needs of the various life stages of paddlefish.
- 4) To develop a model that can predict the ability of the Livingston

Reservoir zooplankton community to support a paddlefish population.

METHODS

Study Site

Livingston Reservoir is located in eastern Texas, approximately 100 km north of Houston and 15 km west of the city of Livingston. The reservoir, which occupies parts of Trinity, Polk, Walker, and San Jacinto counties, covers 90,000 acres, and has the capacity to hold 1.75 million acre-feet of water (Trinity River Authority 1992). The reservoir supplies water to several cities throughout the area, and Houston owns the rights to 70% of its water supply yield (Trinity River Authority 1992).

Livingston Reservoir is located on the Trinity River, which originates near the city of Dallas and runs approximately 885 km into Trinity Bay. Its watershed includes all or part of 37 counties and 46,620 square km (Leifeste 1967). Rainfall for the watershed area ranges from 68 to 132 cm/year (Leifeste 1967). The soil types of the watershed area, which contribute to the water quality of the reservoir, are diverse, ranging from sandy loams to dark, heavy clays (Pitman 1991). The Trinity River is the main source of inflow into the reservoir, although large tributaries such as Harmon Creek, White Rock Creek, and Kickapoo Creek also contribute to the inflow.

Land use in the watershed area is important to the water quality of the reservoir, and includes farming, livestock operations, and various industrial uses (Swearingen 1978). The cities of Dallas and Fort Worth are major contributors of pollutants into the Trinity River north of the reservoir. The development of resort areas and residential communities is also widespread on the reservoir. The reservoir is a major recreational area in the region for fishing, boating, etc.

Zooplankton and water samples were taken from four sites on Livingston Reservoir (Figure 2). At each site, three openwater stations and three backwater samples were sampled.

Site 1. Located on the east side of the reservoir approximately 7 miles north of the dam, in Livingston State Park.

Average openwater depth = 7.9 m

Average backwater depth = 2.5 m

Site 2. Located on the east side of the reservoir near the city of Onalaska, by the Highway 190 bridge.

Average openwater depth = 7.0 m

Average backwater depth = 2.9 m

Site 3. Located approximately four miles east of site 4, in Trinity County.

Average openwater depth = 4.5 m

Average backwater depth = 2.5 m

Site 4. Located between the inflows of Carolina Creek and Newton

Branch, approximately three miles east of the point where the Trinity River enters the reservoir.

Average openwater depth = 15.1 m

Average backwater depth = 7.5 m

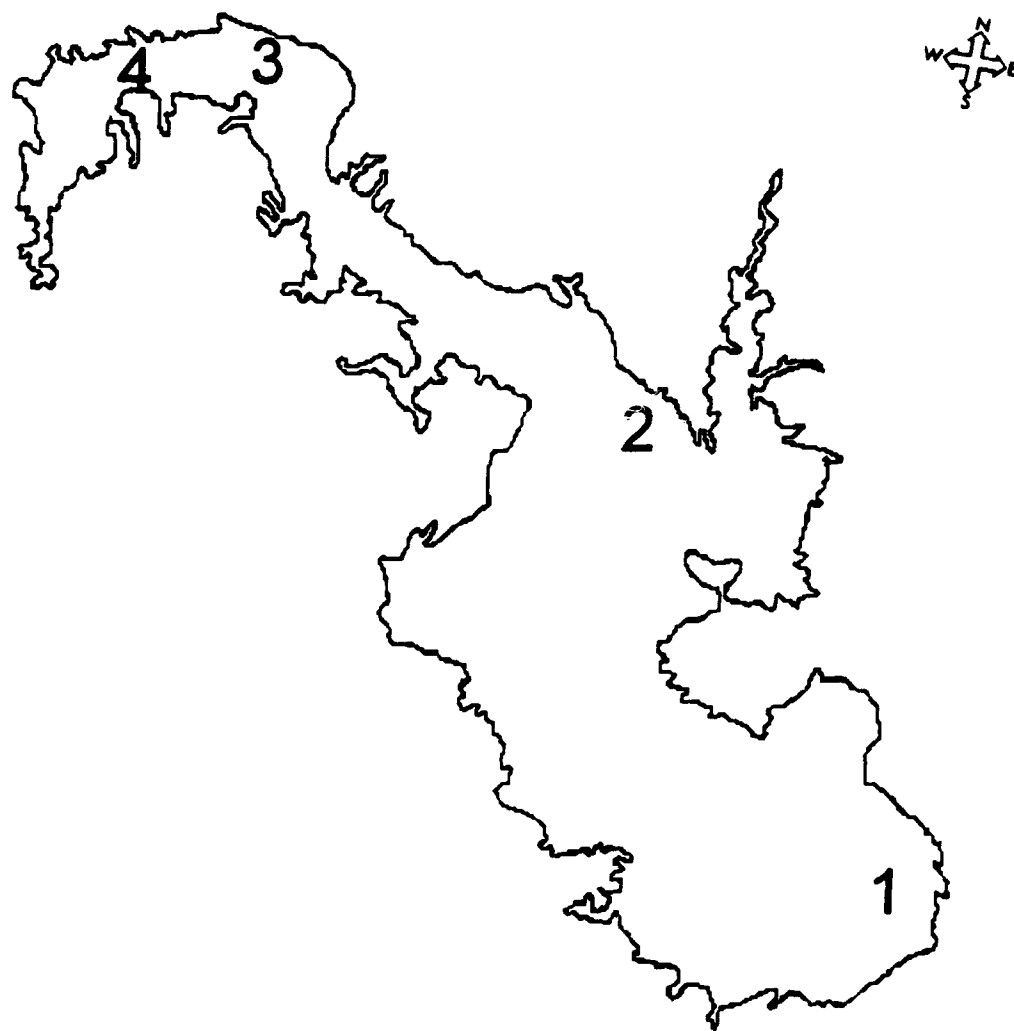


Figure 2. Location of sampling sites for zooplankton and physiochemical parameters on Livingston Reservoir, Texas.

Sampling Schedule

Zooplankton samples were taken twice monthly during the spring and summer (March - September 1992), with the exception of May (Table 1).

Samples were taken once monthly during the fall and winter (October 1992 - February 1993). On each date, four sites, and six stations at each site, (three openwater stations and three backwater stations) were sampled.

Diel samples of zooplankton were taken once each season, with sampling conducted twice per 24-hour period, approximately 12 hours apart. These diel samples were taken only at sites 1 and 2.

Physiochemical Parameters

Physiochemical parameters were measured on the same dates and times as were the zooplankton samples, with the exception of the four night samples, during which no chemical and water quality measurements were made.

Temperature and dissolved oxygen profiles were made at each station using a model 51B oxygen/temperature meter (YSI, Yellow Springs, Ohio). Readings were taken at 1-m intervals from the surface to the bottom. Conductivity readings were taken at 0,2, and 4 m using a model 33 salinity/conductivity/temperature meter (YSI, Yellow Springs, Ohio). A model 5985-80 hand-held digital pH meter (Cole-Parmer Instrument Co., Chicago, Illinois) was used to take pH readings at 0,2, and 4 m. Transparency readings were made with a Secchi disk, and total water depth was measured at each station.

Chemical parameters were measured from water samples taken from one openwater and one backwater station at each site on each date. Turbidity,

Table 1. Sampling dates for zooplankton collection and physiochemical measurements from Livingston Reservoir. No water quality measurements were taken on night samples during diel sampling.

<u>Season</u>	<u>Date</u>
Spring (March - May)	26 March 1992
	8 April 1992
	22 April 1992
	19 May 1992
	8 March 1993 *
Summer (June - August)	5 June 1992
	19 June 1992
	1 July 1992
	22 July 1992
	11 August 1992 *
	25 August 1992
Fall (September - November)	3 September 1992
	20 September 1992
	27 October 1992
	18 November 1992 *
Winter (December - February)	15 December 1992
	8 January 1993 *
	19 February 1993

* = Diel sampling date.

chloride, nitrate, nitrite, ammonia, and phosphate readings were determined using a Hach Drel 2000 water analysis kit, and total alkalinity and hardness were determined using a Hach digital titration kit.

Zooplankton Collection

Zooplankton were collected from three depths (0, 2, and 4 meters) using a Calvert Engineering 3.2-amp continuous-duty submersible pump with a 1.9 cm inlet, calibrated at 30 liters/minute. Samples were taken only at 0 and 2 meters in the backwater stations of sites 2, 3, and 4. Water was pumped through a 1.3-cm diameter hose into a Wisconsin plankton net (80 μ mesh size) for one minute, and the zooplankton were concentrated into a bucket at the bottom of the net. The zooplankton were rinsed from the bucket into a 200-ml or 60-ml bottle and preserved and stained on site with a 10% formalin-rose bengal solution.

Gill Raker Measurement

Gill rakers were removed from five paddlefish taken from the lower Trinity River in May and June of 1993. The paddlefish were between 107 and 114 cm in total length, and weighed between 4.95 and 6.5 kg. The outer gill arch was removed from each paddlefish and preserved in a 10% formalin-rose bengal solution.

The interraker distances between 11 adjacent gill rakers (for a total of 10 measured distances) were measured from both sides of each gill arch using a calibrated ocular micrometer. The distances were measured only from the ventral section of the gill arch, as there is no difference in the interraker distances among different portions of the gill arch (Rosen and Hales 1981). The interraker distance was measured at a point 1-5 mm from the base of the gill

raker, where it attaches to the cartilaginous gill arch.

Interraker distances among the five fish, and the interraker distances among the outside and inside gill rakers, were compared using analysis of variance (ANOVA), and significant differences among specific fish were determined using Tukey's HSD test. All analyses were performed using the SYSTAT 5.0 software package (Wilkinson 1990), and all tests were considered significant at the $p \leq 0.05$ level.

Zooplankton Measurement

Zooplankton were measured to the nearest 0.01 millimeter using an ocular micrometer on an inverted compound light microscope (Swift Instruments International). Three measurements were taken on each organism: 1) Total length (TL) - the length including all spines, setae, etc., 2) Body length (BL) - the length of the body proper (excluding spines, setae, etc.), 3) Width (W) - the width of the body at the widest point. Some organisms, such as members of the cladoceran genera *Bosmina*, *Conochilus*, etc., do not possess spines or setae and, therefore, only two measurements were taken on these organisms.

Zooplankton were measured from 36 samples (one openwater and one backwater sample from each sampling date). The measurements were taken on the following organisms from each sample: 10 adult copepods (including copepodids in late maturity stages), 10 copepod nauplii, 10 cladocerans, and 30 rotifers (10 each of the two most numerous genera, and 10 others). Some samples lacked specific types in such quantities.

Zooplankton Counting and Identification

In order to obtain a count of at least 200 organisms per liter, the samples

were concentrated or diluted by either pipetting off some of the surface liquid in the bottle or by adding water to the sample. An 80- μ m mesh filter was placed over the end of the pipette and rinsed after each use in order to insure that no organisms were drawn into the pipette.

Once concentrated or diluted, the zooplankton in the sample were counted and identified. Two 1-ml counts were made from each sample using a Sedgewick-Rafter cell. Zooplankton organisms identified were of the taxonomic groups Rotifera, Copepoda, Cladocera, and Ostracoda. Identification of organisms was made to genus using taxonomic keys from Ward and Whipple (1959), Eddy and Hodson (1982), Pennak (1989), and Thorp and Covich (1991).

The Quattro Pro 4.0 spreadsheet program (Borland International 1992) was used to compile the data and compute all densities.

All statistical analyses were performed using the Systat 5.0 (Wilkinson 1990) and Statistix 4.0 (Siegel 1992) software programs. Population means for various groupings of zooplankton were compared by season, sampling date, composition, lake site, station, and time of day using a one-way analysis of variance (ANOVA) ($p \leq 0.05$). If differences in means were detected, Tukey's HSD multiple comparisons test was used to determine which means were statistically different.

Determination of Biomass

The biomass of each type of zooplankton measured was determined in micrograms of dry weight per liter (μ g/L) using published length-weight regressions (Dumont et al. 1975). An average weight for each type of organism was calculated using the average body length of each type. This average weight

was multiplied by the density of each type of organism to arrive at an average weight for each type of organism for each sampling date.

Bioenergetics Model Development

A bioenergetics model was developed based upon the assumption that the number of paddlefish that could be supported in the reservoir would be equal to the amount of energy in the reservoir food supply, divided by the metabolic requirements of a paddlefish. The estimated metabolic requirement of paddlefish was based on Peters' metabolic rate equation for poikilotherms (Peters 1983). The energy available in the food supply was estimated from zooplankton biomass estimates made in this study and published estimates of length/ dry weight relationships, and other values in the model were estimated from the literature.

RESULTS

Physiochemical Parameters

Results for all physiochemical parameters measured are included in Appendix I. Pearson correlation coefficients were determined for the relation between each type of zooplankton organism and each physiochemical parameter, and no significant correlations were apparent.

Gill Raker Measurements

I measured the interraker distances on paddlefish to estimate the limits of prey size available to adult paddlefish. The mean interraker distance for all fish was 0.07 mm, with a minimum of 0.03 mm and a maximum of 0.14 mm (Table 2). The range of mean interraker distances in individual fish was 0.06-0.08 mm.

Zooplankton measurements

The mean total length (TL) for rotifers was 0.16 mm, cladocerans, 0.37 mm, nauplii, 0.20 mm, and adult copepods, 0.64 mm (Table 3). The mean body length (BL) for rotifers was 0.13 mm, cladocerans, 0.32 mm, nauplii, 0.18 mm, and copepods, 0.50 mm. The mean width for rotifers was 0.08 mm, cladocerans, 0.20 mm, nauplii, 0.10 mm, and copepods, 0.17 mm.

Composition

The zooplankton community in Livingston Reservoir included representatives from the three main taxa of zooplankton (rotifers, cladocerans, and copepods), as well as isolated individuals from other groups (Table 3).

Twenty-one different genera in the phylum Rotifera were identified. The rotifer community was characterized by *Keratella*, *Brachionus*, *Polyarthra*, *Hexarthra*, *Trichocerca*, and *Synchaeta*. The cladoceran population was made up

Table 2. Distances between paddlefish gill rakers (and standard deviations) (mm). Interraker distances were measured on the inside and outside of the outside gill arch of five adult paddlefish taken from the lower Trinity River, Texas.

	<u>Measurement</u>		
	<u>Inside (Mean)</u>	<u>Outside (Mean)</u>	<u>Total Mean</u>
Fish 1	0.050 (0.012)	0.069 (0.009)	0.059 (0.014)
Fish 2	0.059 (0.010)	0.060 (0.030)	0.059 (0.022)
Fish 3	0.074 (0.011)	0.093 (0.006)	0.083 (0.013)
Fish 4	0.081 (0.021)	0.085 (0.037)	0.083 (0.029)
Fish 5	0.066 (0.012)	0.079 (0.020)	0.073 (0.017)
TOTAL	0.066 (0.017)	0.077 (0.025)	0.072 (0.022)

Table 3. Zooplankton genera identified in Livingston Reservoir, and measurements on selected zooplankton (total length, body length, and width) (mm). Measurements are means for each group.

<u>Organism</u>	<u>n</u>	<u>Measurement</u>		
		<u>TL</u>	<u>BL</u>	<u>W</u>
Rotifer (Total)	975	0.16	0.13	0.08
Cladoceran (Total)	208	0.37	0.32	0.20
Nauplii	353	0.20	0.18	0.10
Adult Copepod (Total)	247	0.64	0.50	0.17
<u>Rotifer genera</u>				
<i>Asplancha</i>	9	0.30	0.30	0.20
<i>Brachionus</i>	261	0.15	0.14	0.10
<i>Cephalodella</i> *	-	-	-	-
<i>Colotheca</i> *	-	-	-	-
<i>Conochiloides</i>	12	0.18	0.18	0.09
<i>Conochilus</i>	21	0.14	0.14	0.07
<i>Filinia</i>	15	0.30	0.11	0.06
<i>Gastropus</i> *	-	-	-	-
<i>Hexarthra</i>	66	0.17	0.13	0.09
<i>Kellicottia</i>	4	0.30	0.11	0.07
<i>Keratella</i>	143	0.18	0.10	0.06
<i>Lecane</i>	1	0.08	0.06	0.04

Table 3. Continued.

<u>Organism</u>	<u>n</u>	<u>Measurement</u>		
		<u>TL</u>	<u>BL</u>	<u>W</u>
<i>Lepadella</i> *	-	-	-	-
<i>Platyias</i>	12	0.18	0.13	0.11
<i>Pleosoma</i>	28	0.15	0.13	0.09
<i>Polyarthra</i>	268	0.15	0.11	0.07
<i>Pompholyx</i> *	-	-	-	-
<i>Synchaeta</i>	40	0.20	0.19	0.15
<i>Testudinella</i>	15	0.13	0.11	0.09
<i>Trichocerca</i>	80	0.16	0.13	0.05
<u>Cladocera genera</u>				
<i>Alona</i> *	-	-	-	-
<i>Bosmina</i>	147	0.25	0.25	0.18
<i>Ceriodaphnia</i>	4	0.49	0.44	0.29
<i>Daphnia</i>	47	0.68	0.54	0.27
<i>Diaphanosoma</i>	10	0.51	0.50	0.27
<u>Copepod genera</u>				
<i>Diaptomous</i>	17	0.64	0.54	0.17
<i>Eurytemora</i>	64	0.77	0.64	0.19
Calanoid copepodids	15	0.32	0.29	0.13
<i>Acanthocyclops</i>	108	0.65	0.46	0.16
<i>Mesocyclops</i>	30	0.66	0.54	0.19

Table 3. Continued.

<u>Organism</u>	<u>n</u>	<u>Measurement</u>		
		<u>TL</u>	<u>BL</u>	<u>W</u>
Cyclopoid copepodids	13	0.51	0.44	0.16

n = number measured, TL = total length, BL = body length, W = width

* = organism that was identified but not measured

mainly of five genera, *Daphnia*, *Bosmina*, *Alona*, *Diaphanosoma*, and *Ceriodaphnia*.

The copepod community was dominated by the nauplii and copepodid stages, but also included adults. The calanoid copepods identified were of the genera *Eurytemora* and *Diaptomous*, while the cyclopoid genera included *Acanthocyclops* and *Mesocyclops*. Some ostracods were found, but because they were so rare they were not identified to specific genera. Each main group included some organisms identified simply as rotifer, cladoceran, or copepod, with the genera being classified as "unidentified."

Density and Distribution

The mean annual density of zooplankton in Livingston Reservoir was 173.5 organisms/L (Table 4). The density by season was: spring, 231.8 org/L; summer, 226.4 org/L; fall, 141.7 org/L; winter, 12.0 org/L (Figure 3). The densities in spring and summer were significantly greater than those in the fall and winter. Maximum densities were found in April (380.7 org/L - April 22) and June (465.1 org/L - June 19), and minimum densities in December (11.6 org/L - December 15) and January (7.7 org/L - Jan 13).

Rotifers made up 77.3% of the total organisms collected, copepods 18.5%, and cladocerans 4.2%, although relative percentages of each type of organism varied with each sampling date (Figure 4). Ostracods were virtually absent, comprising less than 0.05% of all organisms. Because of their extremely low densities, ostracods were not included in further analysis. Because of their numerical dominance, the rotifers strongly influenced the shape of the seasonal density curve for total organisms (Figure 5). Copepods and cladocerans

Table 4. Densities of rotifers, cladocerans, and copepods by sampling date (org/L).

<u>Date</u>	<u>Total</u>	<u>Rotifers</u>	<u>Cladocerans</u>	<u>Copepods</u>
March 26	168.6 (91.6)	100.0 (69.9)	15.3 (13.3)	52.7 (28.2)
April 8	222.7 (155.1)	134.0 (106.1)	20.7 (33.6)	67.9 (58.0)
April 22	380.7 (268.2)	293.2 (268.3)	23.6 (36.8)	63.9 (51.1)
May 19	352.4 (245.5)	233.2 (224.4)	28.3 (38.4)	90.9 (66.2)
June 5	196.1 (149.6)	131.6 (113.5)	13.2 (23.1)	50.9 (61.3)
June 19	465.1 (335.0)	421.4 (319.1)	6.3 (10.2)	37.3 (44.8)
July 1	251.2 (149.1)	229.6 (131.3)	3.3 (8.2)	18.2 (32.0)
July 22	39.4 (27.8)	21.4 (19.2)	3.7 (6.3)	14.3 (15.9)
August 11	289.6 (297.4)	253.9 (202.5)	2.0 (3.1)	33.6 (35.0)
August 25	116.4 (87.1)	97.1 (74.2)	2.3 (3.6)	17.1 (16.0)
September 3	166.9 (109.6)	134.4 (93.5)	2.8 (3.5)	29.7 (22.6)
September 20	201.3 (130.5)	176.0 (121.3)	1.5 (2.3)	24.0 (22.7)
October 27	163.7 (113.2)	127.5 (92.0)	1.7 (3.4)	34.5 (44.1)

Table 4. Continued.

<u>Date</u>	<u>Total</u>	<u>Rotifers</u>	<u>Cladocerans</u>	<u>Copepods</u>
November 18	35.4 (19.1)	18.3 (16.5)	0.9 (1.2)	16.2 (13.1)
December 15	11.6 (9.2)	5.4 (5.4)	1.3 (2.5)	4.9 (3.7)
January 13	7.7 (7.7)	3.4 (3.1)	0.3 (0.4)	4.0 (4.9)
February 19	16.5 (9.1)	10.6 (7.4)	1.2 (0.9)	4.7 (3.0)
March 8	31.2 (23.5)	16.5 (12.2)	3.5 (4.7)	11.2 (12.2)
TOTAL	173.5 (202.1)	134.8 (179.8)	7.3 (18.6)	32.0 (42.8)

Number in parentheses = standard deviation

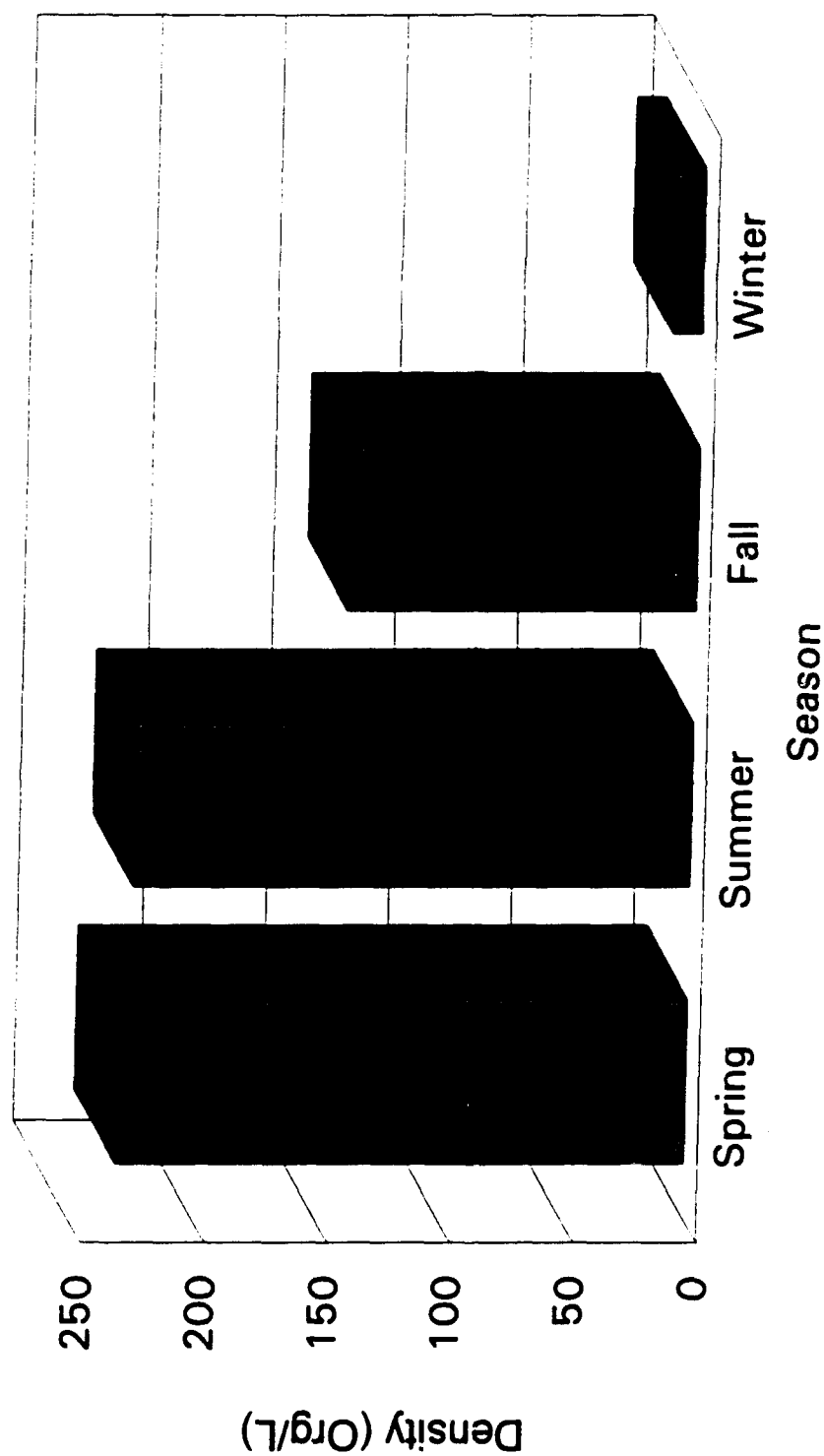


Figure 3. Seasonal density of all zooplankton (rotifers, copepods, and cladocerans combined) sampled from Livingston Reservoir, Texas (March 1992 - March 1993).

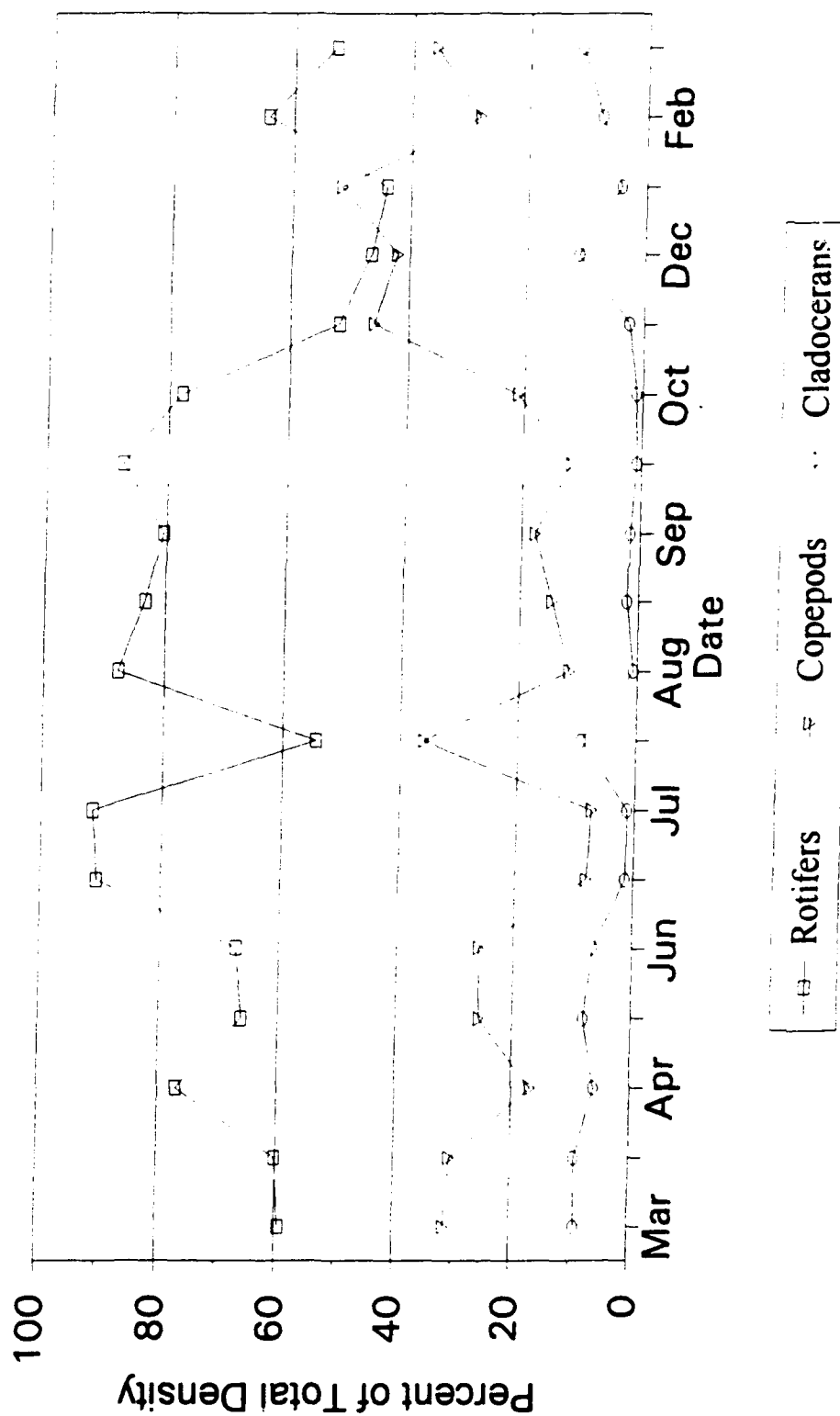


Figure 4. Relative percentage of each type of zooplankton sampled from Livingston Reservoir, Texas (March 1992 - March 1993).

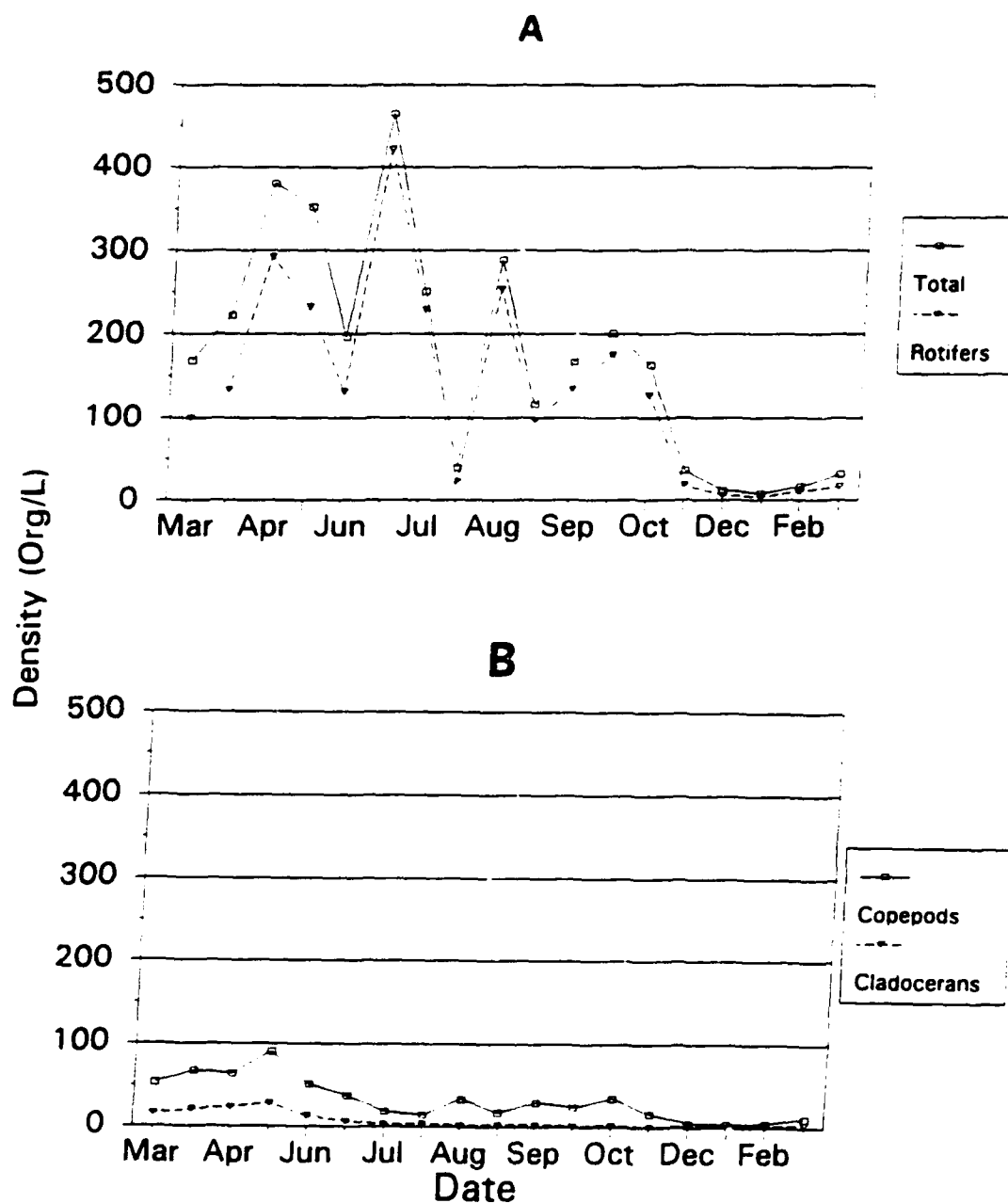


Figure 5. Densities of: A) total zooplankton and rotifers, and B) copepods and cladocerans, for each sampling date measured from Livingston Reservoir, Texas (March 1992 - March 1993).

showed smoother seasonal density curves than did the rotifers or the total zooplankton community (Figure 5). The mean densities for the three main organism types (rotifers, cladocerans, and copepods) were significantly different from each other. Of the copepods, nauplii accounted for 93.5% and copepodids made up 4.5% (Figure 6). Rotifers and copepod nauplii together made up 95% of the zooplankton.

The mean zooplankton density by site on the reservoir was: site 1, 127.9 org/L; site 2, 243.3 org/L; site 3, 217.9 org/L; site 4, 114.4 org/L (Figure 7). Sites 2 and 3 had significantly higher densities than did sites 1 and 4.

The mean density at openwater stations was 182.8 org/L, while the mean density at cove stations was 161.0 org/L, but the differences in densities were not statistically significant. The differences between openwater and backwater stations were more pronounced for rotifers than for either copepods or cladocerans.

Diel zooplankton samples were taken on four dates, one for each season. The largest difference between night and day densities at the surface was during the August sample (Figure 8), but there was no significant difference for all organisms combined on any of the dates. When the different types of organisms were separated, however, some significant differences became apparent. Cladocerans showed the most significant increases in densities at the surface from day to night, with significance during August, November, and March (Figure 9). Copepods showed a significant increase in density from day to night during August (Figure 10), while rotifers were never significantly more abundant during the night.

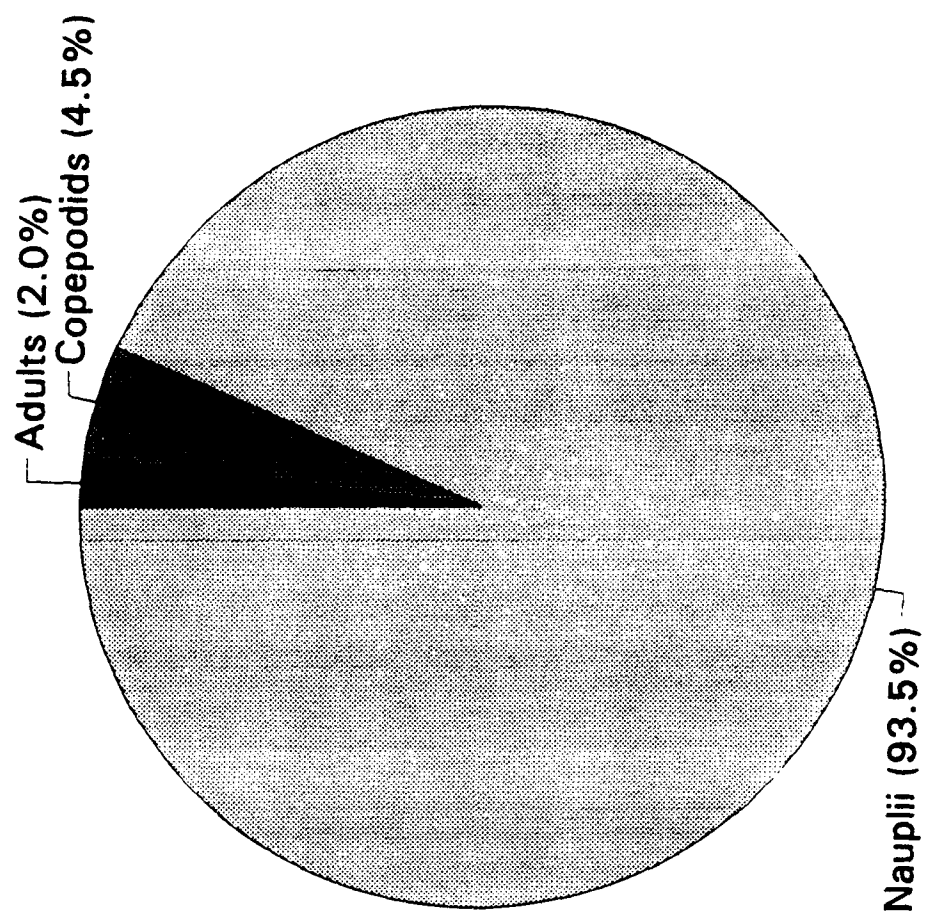


Figure 6. Percentage of total copepod density of each copepod maturity stage from Livingston Reservoir, Texas (March 1992 - March 1993).

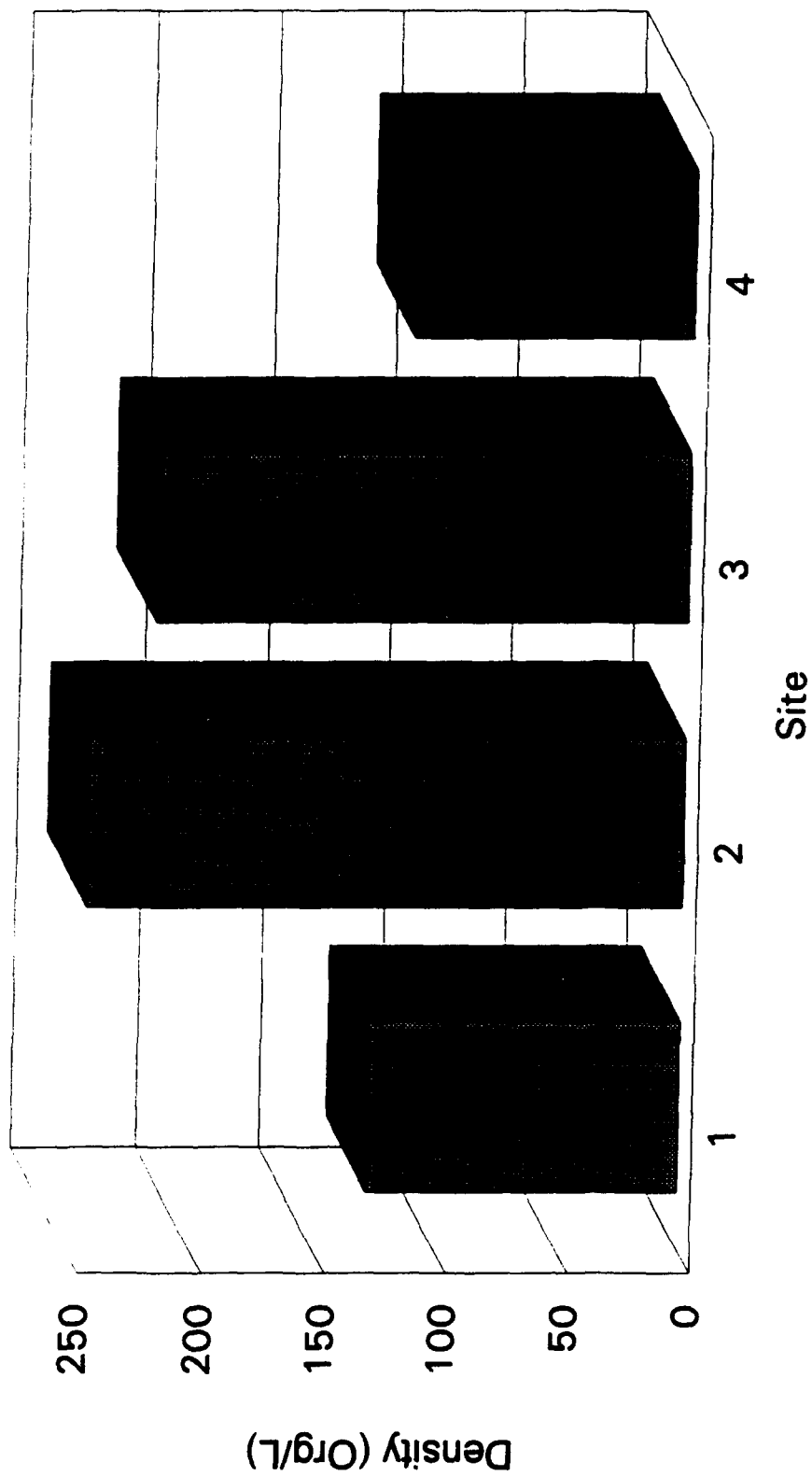


Figure 7. Densities of all zooplankton (rotifers, copepods, and cladocerans combined) at sites 1-4 on Livingston Reservoir, Texas (March 1992 - March 1993).

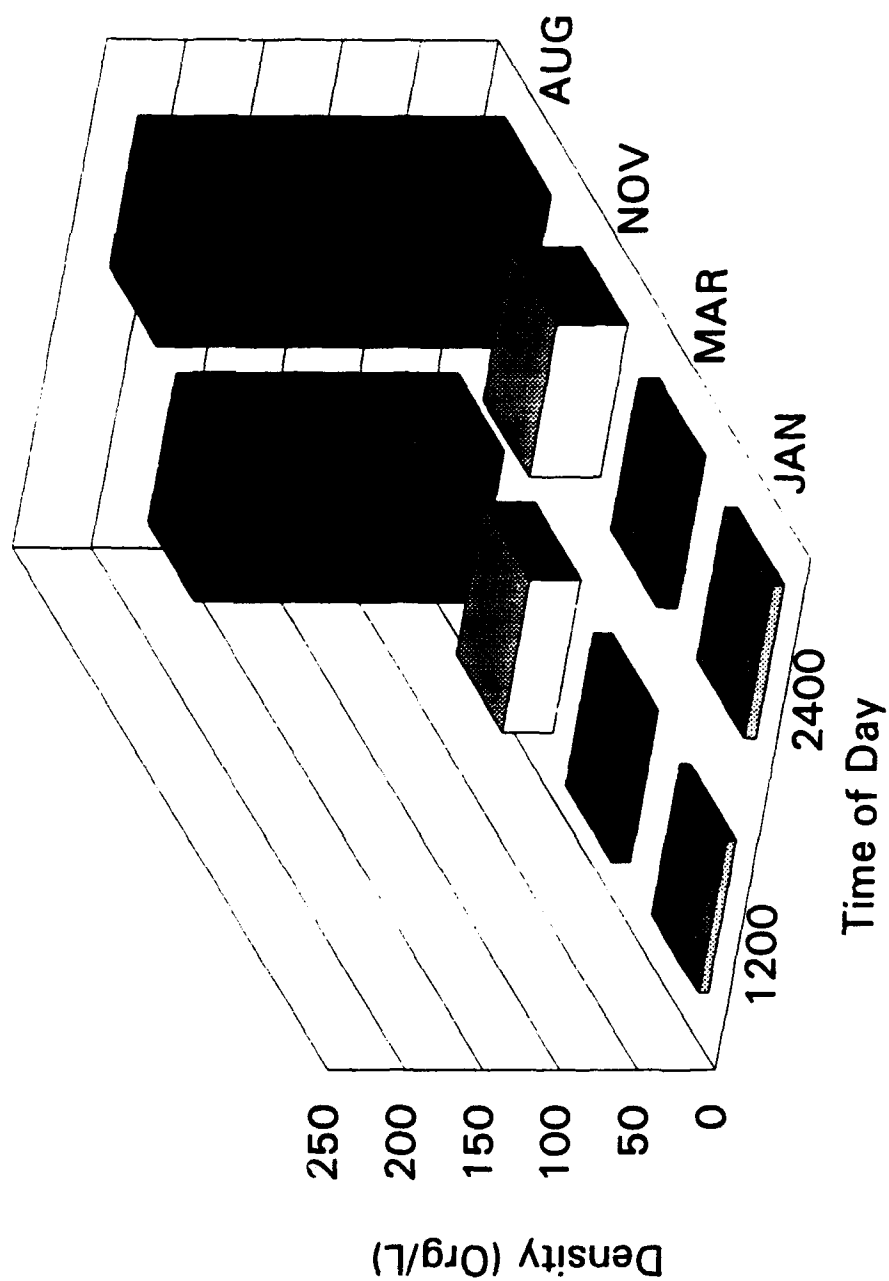


Figure 8. Densities of all zooplankton (rotifers, copepods, and cladocerans combined) during day (1200) and night (2400) samples from Livingston Reservoir, Texas.

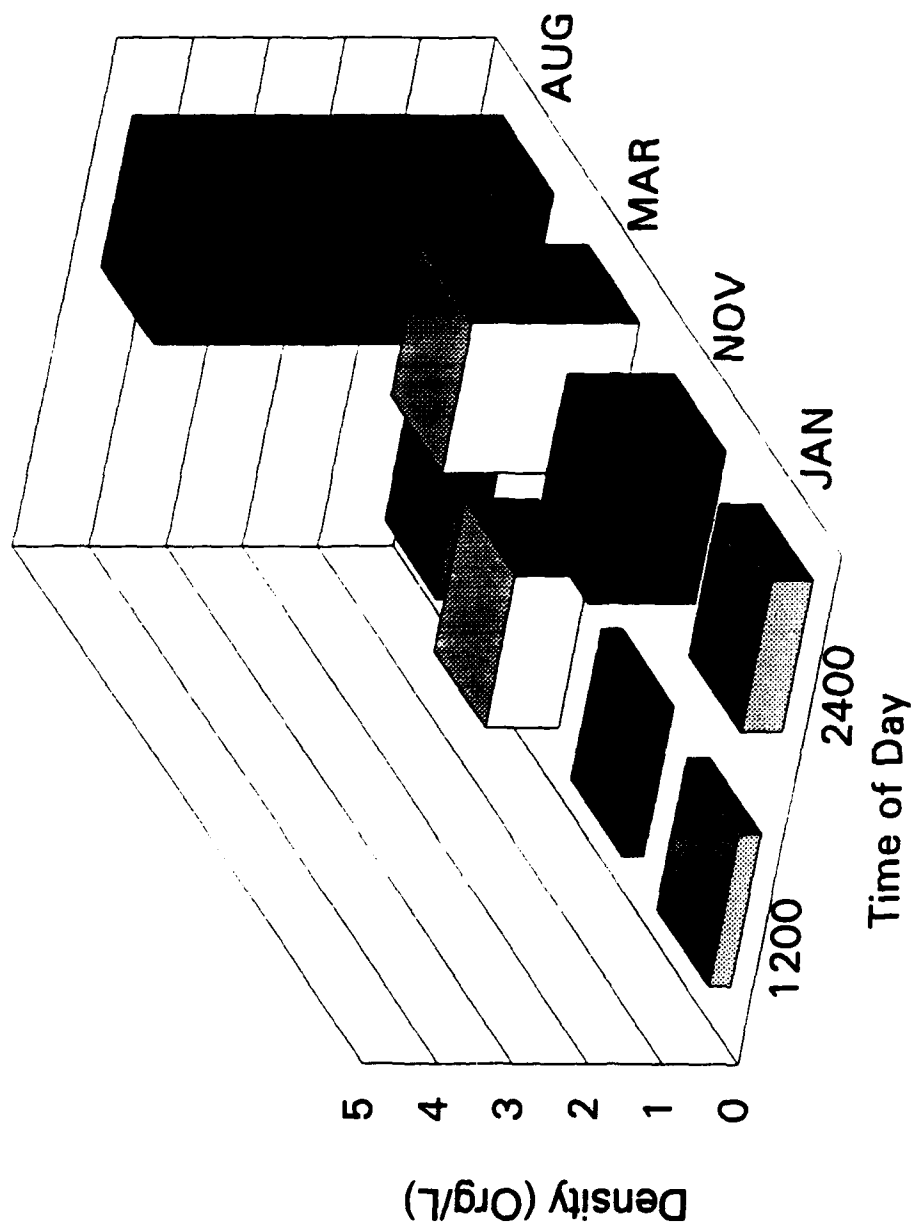


Figure 9. Densities of cladocerans during day (1200) and night (2400) samples from Livingston Reservoir, Texas.

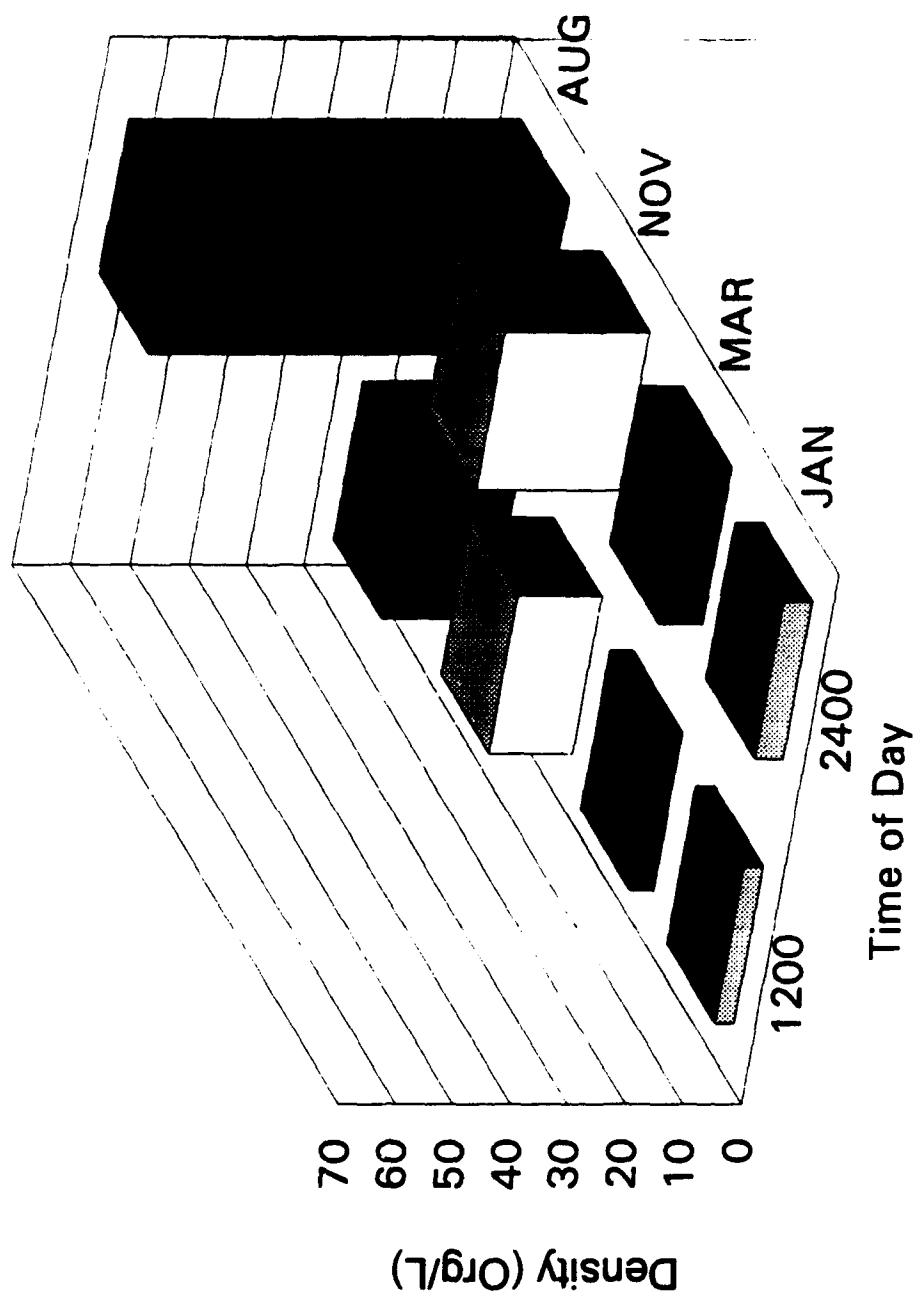


Figure 10. Densities of copepods during day (1200) and night (2400) samples from Livingston Reservoir, Texas.

Biomass

The average dry weight (μg) for a single rotifer was 0.093; cladoceran, 0.787; adult copepod, 1.518, and nauplii, 0.210. The mean annual weight ($\mu\text{g/L}$) for the rotifer community was 12.4; cladocerans, 5.8; adult copepods, 7.5; and copepod nauplii, 5.7 (Table 5). Rotifers made up 40% of the total biomass; cladocerans, 18%; adult copepods, 24%; and nauplii, 18% (Figure 11)., although the percentage biomass made up by each type of organism varied with each sampling date (Figure 12).

Table 5. Biomass of rotifers, cladocerans, adult copepods, and copepod nauplii (μg dry weight), determined from published length/weight regressions (Dumont et al. 1975).

<u>Date</u>	<u>Rotifer</u>	<u>Cladoceran</u>	<u>Copepod</u>	<u>Nauplii</u>
March 26	7.27	3.97	11.83	8.36
April 8	13.21	17.31	8.05	14.72
April 22	31.96	15.13	14.15	1.93
May 19	17.72	36.82	38.97	11.31
June 5	12.04	3.98	0.97	6.50
June 19	50.36	2.09	0.65	5.12
July 1	21.46	1.54	2.24	3.58
July 22	2.30	0.98	7.21	1.66
August 11	20.11	0.23	0.20	4.92
August 25	8.30	0.51	1.12	2.69
September 3	9.37	0.47	1.00	3.84
September 20	14.47	6.17	2.93	4.09
October 27	11.78	1.93	4.58	5.80
November 18	2.04	1.00	6.09	4.05
December 15	0.56	0.79	0.91	0.64
January 13	0.39	0.45	3.68	0.68
February 19	0.89	0.89	3.04	0.93
March 8	1.57	3.58	10.16	2.16
TOTAL	12.42	5.77	7.52	5.68

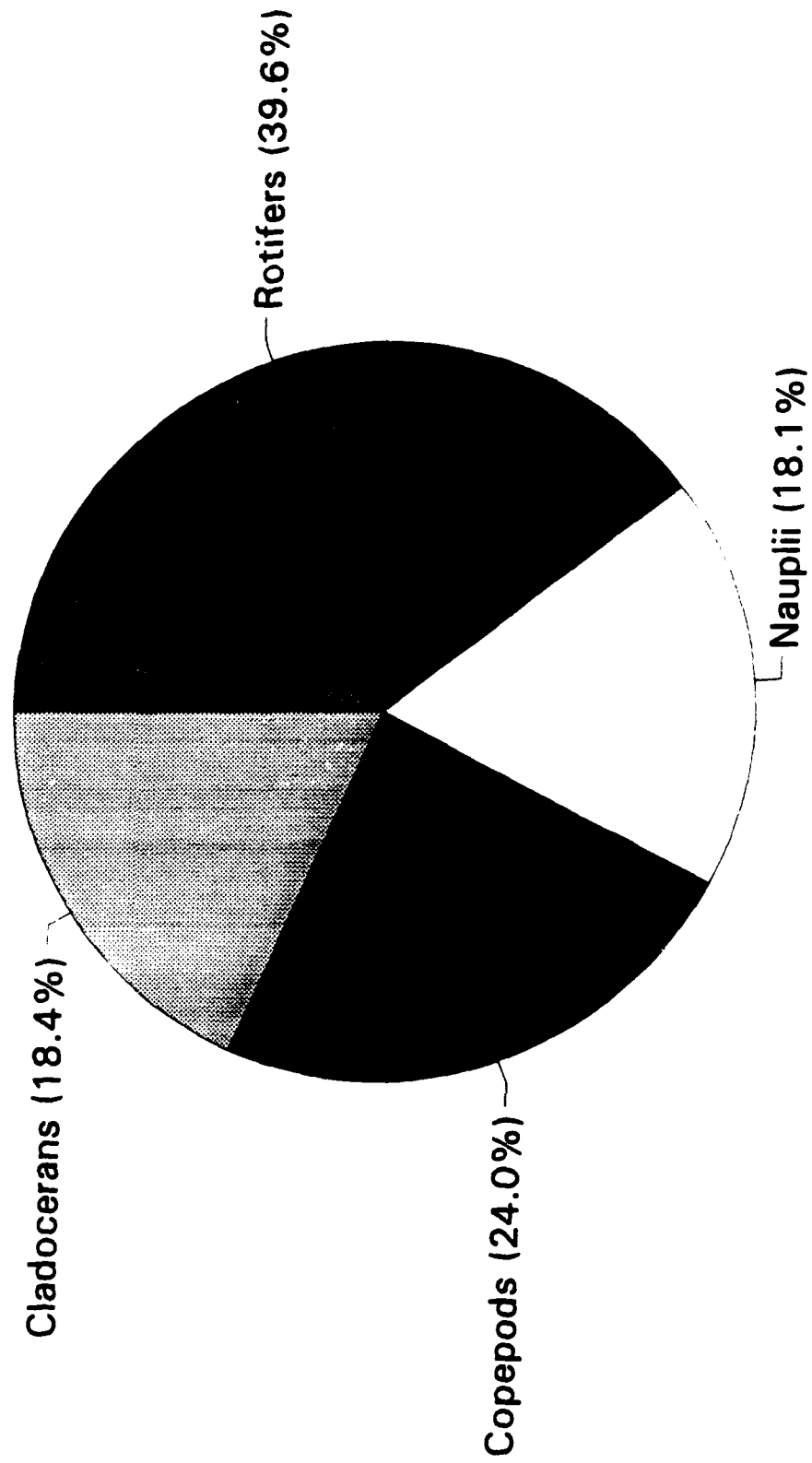


Figure 11. Percentage of total biomass for each type of zooplankton measured from Livingston Reservoir, Texas.

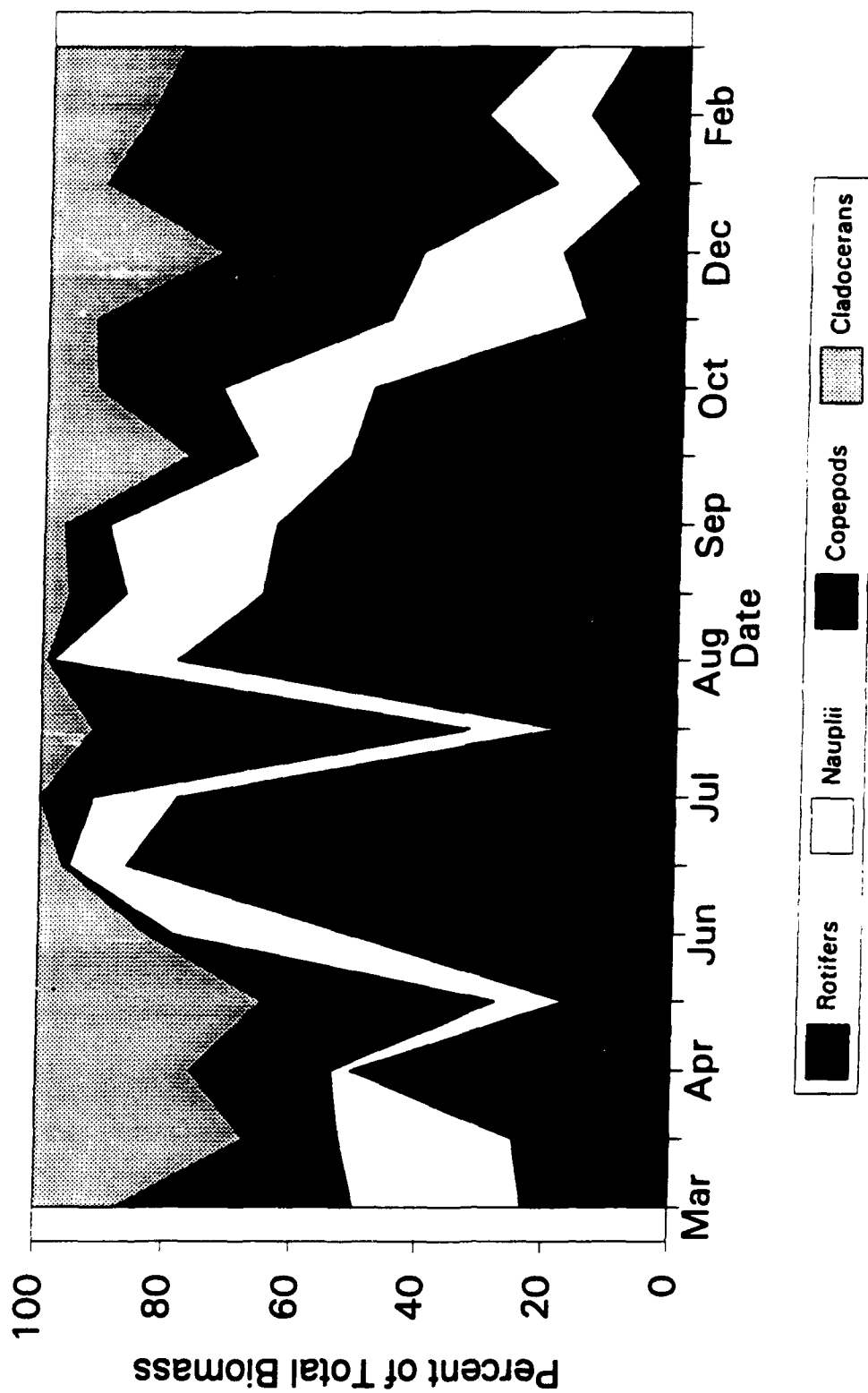


Figure 12. Relative percentage of total biomass for each type of zooplankton for each sampling date from Livingston Reservoir, Texas.

DISCUSSION

Physiochemical Parameters

The effects of different levels of several physiochemical parameters, and the ideal range of such parameters, have been determined for paddlefish. Water temperatures must be between 10°-20° C for paddlefish to spawn, and eggs are successfully incubated at water depths from 0.3-30 m (Hubert et al. 1984). Adult paddlefish will survive in water temperatures of 0.6°-30° C, depths of greater than 0.9 m, and dissolved oxygen (DO) concentrations of greater than 0.5 mg/L (Hubert et al. 1984). The pH range suitable for paddlefish is between 6.5-8.2, and paddlefish can survive at chloride levels less than or equal to 170 mg/L (Pitman 1991).

All physiochemical parameters are within established paddlefish survival ranges (Hubert et al. 1984, Pitman 1991), with the exception of pH levels. In 33% of the samples measured, pH levels were found to be on the high end of the paddlefish survival range. Because they are probably the result of local algal blooms that paddlefish are probably able to avoid, these high pH levels are most likely not critical to survival of the paddlefish in the reservoir.

Zooplankton are sensitive to different levels of certain physiochemical parameters as well. The reproductive rates of rotifers and copepods have been positively correlated with water temperatures (Edmondson 1965; Williamson and Butler 1987). Low pH levels can be lethal to cladocerans, and rotifers can be classified into three pH types that describe pH ranges that each type prefers (Wallace and Snell 1991). High acidity levels can reduce the number of zooplankton species in a lake, and alkalinity levels have been correlated with

copepod abundances and sizes (Hazelwood 1961). Both rotifers and copepods are able to survive at low DO concentrations, at least for some time (Wallace and Snell 1991; Williamson 1991). The effects of such physiochemical parameters upon zooplankton communities is highly variable and localized, though, and the zooplankton community of Livingston Reservoir did not seem to be correlated with any of the physiochemical parameters measured.

The overall water quality of Livingston Reservoir seems sufficient to harbor both a paddlefish population and a zooplankton population upon which the paddlefish feed. The influent water from the Trinity River, which is heavily influenced by the Dallas/Fort Worth area, does not seem to have a strong negative impact upon water quality, as the alkalinity, hardness, and nitrogen- and phosphorus-compound levels are not significantly different in the areas of the reservoir nearest to the river than those in other areas.

Paddlefish Food Resources

Although the number of fish examined for interraker distance was relatively small (5), the results indicate a range of mean interraker distances (0.06-0.08 mm) consistent with those reported in previous literature (Rosen and Hales 1981, Pitman 1991). Rosen and Hales (1981) studied paddlefish gill rakers and found the range of mean interraker distances to be 0.06-0.09 mm. They found no significant differences between interraker distances among gill arches on the same fish, location of the gill raker on the gill arch, or fish of different ages (Rosen and Hales 1981).

The measurements of the zooplankton revealed that the overall sizes of organisms in Livingston Reservoir are relatively small. Rotifers can range in

length from 0.04-2.5 mm, with the majority being between 0.1-0.5 mm (Pennak 1989), while the rotifers in this study ranged from 0.08 mm to 0.30 mm in total length. Cladocerans usually range in length from 0.20-18.0 mm (Dodson and Frey 1991), while the mean lengths of cladocerans in this study ranged from 0.25-0.68 mm. The range of lengths of copepods is usually from less than 0.5 mm to 2.0 mm (Williamson 1991), while the mean range of copepod lengths in this study was 0.32-0.77 mm.

Although the zooplankton in Livingston Reservoir are relatively small, they are still, on the whole, larger than the interraker distances of the paddlefish. Paddlefish are therefore capable of capturing and utilizing all zooplankton in the reservoir. The rotifers and copepod nauplii, though, are significantly smaller than the cladocerans and adult copepods, and therefore will most likely be consumed inefficiently by the paddlefish for two reasons. First of all, small zooplankton organisms could be excluded from capture by the gill rakers by encountering the gill rakers in different physical orientations. The widths of the rotifers and smaller copepod nauplii, as opposed to the lengths, are very close to, and sometimes smaller than, the interraker distances of the paddlefish. When these organisms approach the gill rakers so that their width, rather than their length, is perpendicular to the gill raker, the effective size of the organism is the width. When this situation occurs, the organism will likely pass through the gill raker and not be consumed by the paddlefish. Such a situation might also occur when the organism approaches the interraker space headfirst or tailfirst, causing the effective size of the organism to be its breadth. MacNeill and Brandt (1990) found that the probability of capture of small copepods by alewives was 36.3%

based on width of the copepod, 0% based on breadth, and 100% based on length. They also demonstrated that the overall retention efficiency is lower when based on a composite of length, width, and breadth of an organism than when based on length alone (MacNeill and Brandt 1990). The hydrodynamics and particle orientation as the water passes through the gill rakers is important to the ability of paddlefish to retain, and therefore utilize, different size classes of zooplankton, and is in need of further experimental research.

A second reason why small rotifers are most likely utilized less efficiently by paddlefish than are larger zooplankton is that smaller rotifers could be excluded from capture by paddlefish by the physical structure of the rotifers' bodies. Most rotifers are relatively soft and flexible, lacking the hard carapace of cladocerans and the exoskeleton of copepods (Wallace and Snell 1991, Dodson and Frey 1991, Williamson 1991). Therefore, given the smaller size of the rotifers, and the speed of the water current flowing through the gill rakers, it is likely that the bodies of rotifers can constrict and bend when in contact with the relatively rigid gill rakers, and therefore, pass through the interraker space (MacNeill and Brandt 1990).

Previous research on the food resources of paddlefish supports the idea that paddlefish do not consume rotifers and other small zooplankton to a large extent. Rosen and Hales (1981) reported that the vast majority of paddlefish food resources include only crustacean zooplankton and that smaller zooplankton, such as rotifers and copepod nauplii, are virtually absent from their diet. They also noted that the average minimum length of retained organisms was 0.20-0.25 mm, which is somewhat larger than the minimum interraker

distance (0.06-0.09 mm) (Rosen and Hales 1981). In a review of paddlefish in Texas, Pitman (1991) states that "almost entirely absent in adult paddlefish diets are small nauplii, rotifers, cyclopoid copepods, etc. . . ." In a study of zooplankton population responses to paddlefish feeding, rotifer populations increased in response to the presence of paddlefish, due to heavy predation upon the larger zooplankton by the paddlefish, and the subsequent decreased competition with rotifers (Burke and Bayne 1986). Such studies support the conclusion that, even though the gill rakers of paddlefish seem physically able to retain small rotifers and nauplii, such organisms are not being utilized to a large extent.

An alternative possibility to the hypothesis that paddlefish do not utilize small zooplankton efficiently is that the smaller rotifers and copepod nauplii are utilized by paddlefish, but that they are not found in the stomach contents of the fish studied. Because of the soft-bodied structure of most rotifers, they may be digested more quickly than cladocerans and copepods. Therefore, the time that has elapsed between a fish's last meal and its time of capture and preservation would likely influence the relative abundance of rotifers found in the analysis of its stomach. Rosen and Hales (1981) addressed this problem by analyzing the contents of only the anterior one-third of each paddlefish stomach, in which the zooplankton would not have been subject to much digestive activity, and still found very few rotifers and smaller copepods. Such a result supports the original hypothesis that rotifers and nauplii are not being consumed by paddlefish rather than the idea that they are simply not showing up in the stomach analyses.

The diets of several other filter-feeding fish have been studied as well.

MacNeill and Brandt (1990) measured gill rakers in the alewife, a filter-feeding clupeid, and the interraker distances in the alewives were similar to the interraker distances in paddlefish. It has been shown that rotifers are an infrequent part of the alewife diet (Mills et al.1992). Gizzard shad and threadfin shad, both filter-feeding planktivores, have been shown to have no effect on the abundances of some small rotifer species (Guest et al.1990).

The overall conclusion is that the majority of the zooplankton in Livingston Reservoir are larger than the distance between gill rakers of a paddlefish. Therefore, the paddlefish are able to capture all zooplankton taxa in the community, but will capture the rotifers and nauplii less efficiently than the adult copepods and cladocerans due to the relatively small sizes and soft body structure of the rotifers and nauplii.

Zooplankton Community Structure

Composition

The genera found in Livingston Reservoir are consistent with those found in other Texas reservoirs. Rogers (1976) studied Striker Creek and Murval Reservoirs in east Texas, and found the rotifers *Brachionus*, *Conochiloides*, *Conochilus*, *Keratella*, and *Polyarthra*, along with the cladoceran *Bosmina*, and cyclopoid and nauplii copepods. A study on the Trinity River above Livingston Reservoir found the rotifer genera *Keratella*, *Filinia*, *Kellicottia*, and *Lecane*, the cladocera *Bosmina*, *Moina*, and *Chydorus*, and the copepods *Tropocyclops*, *Cyclops*, and *Mesocyclops* (Swearingen 1978). The dominant rotifers in Livingston Reservoir in 1978 were *Brachionus*, *Polyarthra*, *Synchaeta*, *Keratella*, and *Trichocerca* (Swearingen 1978). *Bosmina* dominated the cladoceran

community in the reservoir, and copepod nauplii made up the majority of the copepod community (Swearingen 1978).

The rotifer community described in this study is diverse, with more than 20 genera identified. The copepod and cladocera communities are less rich, with only 5 cladocera and 4 copepod genera represented. The limited number of cladoceran and copepod genera in the reservoir is not surprising, as zooplankton communities are usually dominated by one or two species of cladocera, and one dominant cyclopoid and calanoid copepod (Pennak 1989, Dodson and Frey 1991).

Density

The mean annual density of 173.5 org/L, along with the seasonal densities, are higher than those reported for other Texas reservoirs. Allard (1974) found a mean zooplankton density of 56 organisms/liter in Sam Rayburn Reservoir in east Texas. A study of White Rock Lake near Dallas showed average rotifer densities of 120 organisms/liter (Swearingen 1978). Swearingen (1978) found the average zooplankton density of Livingston Reservoir to be 63.1 organisms/liter.

A possible factor contributing to differences in these studies is the sampling method. Zooplankton samples can be taken using a net tow or a pump. I used the pumping method to obtain samples from specific depths, which is difficult to accomplish with a net tow. But, certain types of zooplankton exhibit escape behavior that may enable them to escape being drawn into a pump (Williamson 1987). The organisms that exhibit such behavior are usually the cladocerans and copepods, which are stronger swimmers than the

smaller rotifers. Therefore, it is possible that my pumping method resulted in relatively fewer of the larger organisms than were actually present in the water. Icanberry and Richardson (1973) compared pumping methods over a wide range of pumping rates with netting methods, and found no difference between the two methods in efficiency of capturing, or mortality of, adult copepods and other zooplankton organisms capable of substantial motility. In a review of pumping methods, Powlick et al. (1991) found that pumping methods had similar, and in some cases better, efficiencies of capture for copepods than did nets. Therefore, the pumping method used most likely did not result in an underestimation of the larger, more motile cladocerans and copepods.

It may be of significance to paddlefish that the zooplankton community of Livingston Reservoir is dominated in numerical terms by small zooplankton organisms. Rotifers and nauplii together make up 95% of all zooplankton organisms in the community, and the small cladoceran and adult copepod populations are dominated by smaller members of these groups. Because paddlefish grow best by feeding upon larger zooplankton organisms, limited food resources may be available to the paddlefish population.

The absence of larger zooplankton organisms in the reservoir could be attributed to several factors. The classic model of zooplankton size structure suggests that smaller organisms thrive when larger organisms are removed through predation, mainly by planktivorous fish (Gilbert 1988). According to this model there must be an abundance of predation upon larger zooplankton organisms in this community. Such a conclusion seems likely, as planktivorous fish, such as gizzard and threadfin shad, are numerous in Livingston Reservoir

(Klussman et al. 1987). Other fish, such as crappie, largemouth bass, and bluegill, also are present in the reservoir, and the larval forms of these fish are particulate zooplankton feeders that select larger zooplankton (DeVries and Stein 1992). Dettmers (1992) and DeVries and Stein (1992) showed that shad reduce densities of larger zooplankton, thus leading to an increase in smaller organisms. Therefore, the presence of these other fish may have a detrimental effect upon the paddlefish, both by competing directly for larger zooplankton and by changing the size structure of the zooplankton community.

One way such predation could cause the relatively high densities of smaller organisms can be explained by the size-efficiency hypothesis, first proposed by Brooks and Dodson (1965). This hypothesis suggests that all herbivorous zooplankton compete for the same food resources, but larger zooplankton feed more efficiently by consuming a larger range of food particles. Therefore, when predation upon the larger organisms is low, the smaller ones will be outcompeted and eliminated, but when predation is high on the larger organisms, they will be eliminated, thus allowing the smaller ones to thrive. In the presence of the numerous planktivorous fishes in Livingston Reservoir, the larger zooplankton are probably being removed at relatively rapid rates, thus leading to the dominance of small zooplankters.

The size-efficiency hypothesis might not be the best explanation for the size structure of the zooplankton community, though, because the theory has not been supported by much experimental evidence. Several experiments on the response of smaller rotifers to the presence of larger organisms showed that rotifer densities were suppressed by larger *Daphnia*, but were not affected by the

presence of larger copepods, which should also be competing with the rotifers for food (Gilbert 1988, Neill 1984). One of the original authors of the hypothesis, S.I. Dodson (1974), states that the hypothesis is supported only by "anecdotal" evidence, and that the relationship between abundances of small and large zooplankton organisms might be caused by factors other than competition for food resources between the two.

Another possible reason for the high density of smaller zooplankton in the reservoir is that high predation upon the larger zooplankton by planktivorous fish could be decreasing predation upon rotifers. Diaptomid copepods, which are present in Livingston Reservoir, have been shown to feed upon rotifers (Williamson 1987). Some cladocerans, although they do not prefer rotifers, also feed on rotifers (Williamson 1983). Some predacious rotifers, such as *Asplancha*, also were present in the samples taken from Livingston Reservoir. Therefore, removal of these predacious zooplankton organisms might lead to increased rotifer density not through the reduction of exploitative competition for food, but through the reduction of predation upon the rotifers by other zooplankton.

Predation by other invertebrates also might contribute to the small size structure of the zooplankton community. Neill (1981) showed that *Chaoborus* decreased densities of larger cladocerans by size-selective predation. Moreover, some species of *Daphnia* actually will undergo morphological reductions in size in response to predation by the invertebrate *Notonecta* (Dodson and Havel 1988).

Based on the previous discussion on the effects of planktivores upon zooplankton size structure, it is possible that paddlefish are eating large numbers

of larger organisms, and thus driving down the size structure of the zooplankton community themselves. This would be an ideal situation for the paddlefish in Livingston Reservoir, as it would indicate a suitable food supply, but it is not likely. Paddlefish predation has been shown experimentally not to reduce populations of large *Daphnia* (Michaletz et al. 1983). Also, a study of zooplankton in Livingston Reservoir before paddlefish were stocked in the reservoir found lower zooplankton densities than did this study, but showed similar compositions (Swearingen 1978). If the paddlefish were responsible for the present densities in the reservoir, we would expect that the species composition would be different, and the densities lower, than before so many additional paddlefish were added to the reservoir (Burke and Bayne 1986). One thing is clear: as particulate feeders, juvenile paddlefish are dependent upon larger zooplankton organisms, and the lack of such organisms can cause adverse effects upon their growth and survival (Michaletz et al. 1983). Negative impacts upon juvenile paddlefish would, in turn, have serious effects upon the establishment of a healthy adult population and the ability of Livingston Reservoir to support a paddlefish population.

Although the small rotifers and nauplii dominated the zooplankton community in numerical terms, it is necessary to look at the relative proportion of each type of organism in terms of the biomass of the community. The relative biomass of each type of organism is significant to the paddlefish because it represents the amount of energy available as a food source. Figure 12 shows that rotifers make up only 40% of the biomass of the zooplankton community, compared to almost 75% of the community in terms of relative density.

Cladocerans and copepods make up 18% and 24%, respectively, of the biomass, and therefore make up a larger percentage of the total biomass than of the relative density. But rotifers still represent the largest amount of biomass available in the zooplankton community. And, when the 18% of the biomass represented by the copepod nauplii is considered, the smaller organisms upon which paddlefish do not feed as efficiently make up almost 60% of the total biomass of the Livingston Reservoir zooplankton community. So, although the cladocerans and copepods that paddlefish need to feed upon do make up a larger proportion of the biomass than they do relative density, the smaller rotifers and copepod nauplii still make up the majority of the available energy in the zooplankton community. In addition, since even the cladoceran and copepod communities in Livingston Reservoir are made up of smaller organisms within these classes, the paddlefish will feed less efficiently even upon these communities.

The overall effect of the small size structure of the zooplankton community in Livingston Reservoir upon paddlefish is difficult to assess. It would be advantageous to the paddlefish to have a large supply of larger organisms, due to the high amounts of energy available in such sources and to their ability to more efficiently capture and utilize such organisms. But, because of their ability to utilize smaller crustacean zooplankton and rotifers, such a food source would be suitable if found in sufficient numbers. However, the densities of the smaller zooplankton were not significantly higher than those found in other paddlefish habitats, and the densities of the larger ones were much lower. However, even the larger copepods and cladocerans are relatively small

compared to overall size ranges for cladocerans and copepods. Therefore, based upon the size structure and overall densities of the zooplankton community, the food resources in Livingston Reservoir seem less than optimal for a substantial paddlefish population.

Seasonal Density

The overall cycle of density for zooplankton in Livingston Reservoir for 1992-1993 reveals a common cycle of increasing densities in the spring and decreasing densities through the summer, fall, and winter. The pattern is disturbed by erratic population pulses between June and August. Such pulses are common, and it is because of such sudden shifts in zooplankton populations that we took samples twice monthly during the spring and summer. When the populations for those months in which two samples were taken are averaged together for each month, the density curve over the entire year smoothes out considerably (Figure 13). Figure 5 shows the seasonal densities of each of the three types of zooplankton, and reveals that the overall density pattern is heavily influenced by the numerical domination of rotifers. Copepods and cladocerans show a much smoother population curve than do the rotifers.

Zooplankton population dynamics, including annual variations in densities such as the ones in this study, are extremely variable and are influenced by a vast array of factors, including predation, abiotic influences (temperature, dissolved oxygen, water chemistry, light intensity, introduced substances and chemicals), food quality and quantity, and competition. Because of the great number of influences, it is impossible to attribute fluctuations in a population to a single factor, but instead, such fluctuations are the result of several combined

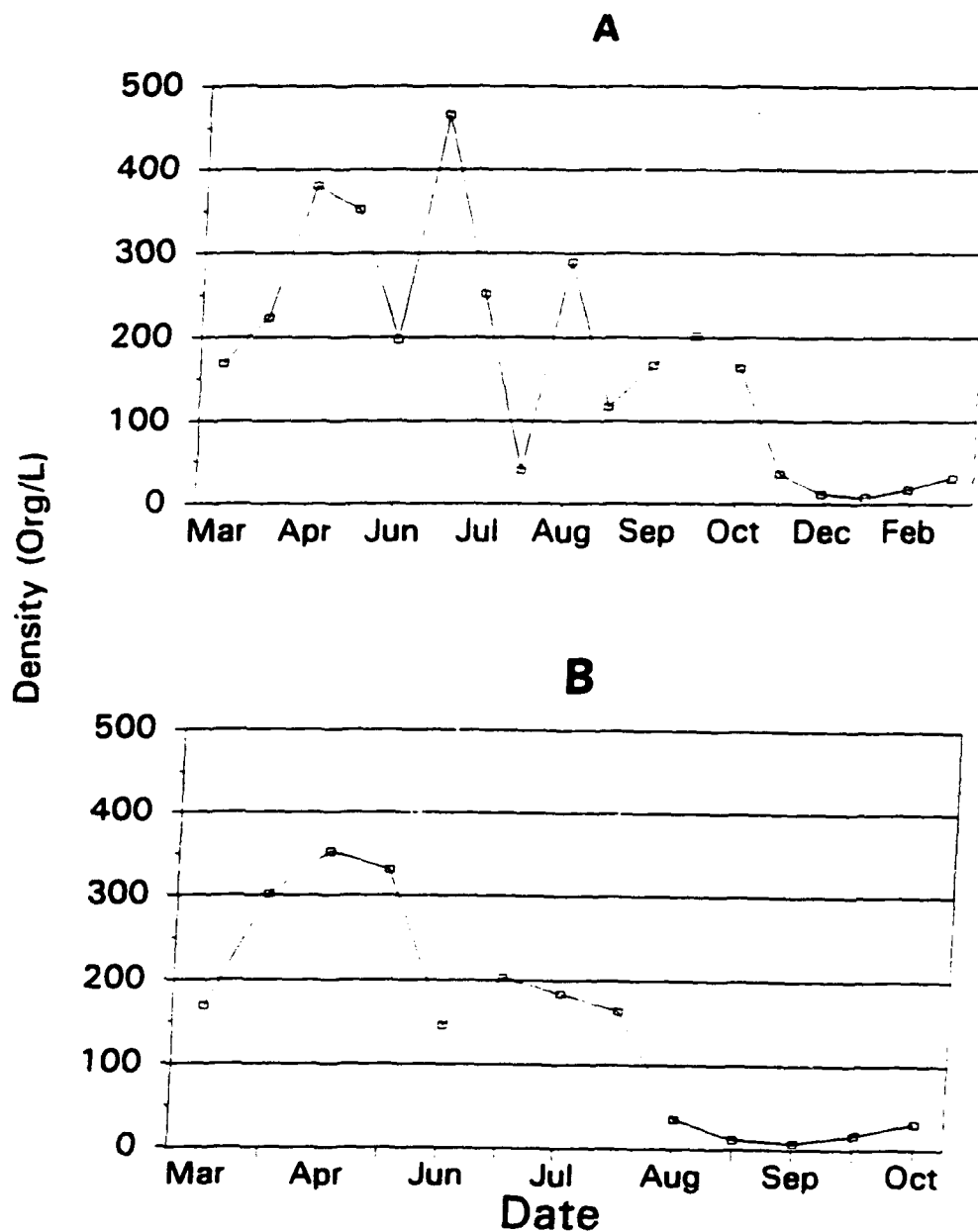


Figure 13. Densities of total zooplankton for: A) each sampling date, and B) monthly means, measured from Livingston Reservoir (March 1992 - March 1993).

factors. One main influence, though, is the cycle in availability of phytoplankton as food sources. Because of their heavy dependence upon phytoplankton, cladoceran growth rates are especially coupled to phytoplankton availability. Phytoplankton usually experience a bloom in the spring, as water temperatures, light availability, and nutrient levels increase, which subsequently causes an increase in the zooplankton biomass (Pennak 1989).

Distribution

Comparing the density of zooplankton at the four sites sampled on the reservoir can give an indication of the horizontal distribution of zooplankton in the reservoir. Figure 7 shows that zooplankton densities are highest at Sites 2 and 3, and least abundant at Sites 1 and 4. The distribution in Livingston Reservoir follows the model of reservoir zooplankton distribution described by Marzolf (1990) in which the horizontal distribution of zooplankton is influenced by the hydrodynamics and resource availability of the reservoir and the river feeding into it. At the point near where the river enters the reservoir (site 1), the current velocity is too great for the zooplankton to reproduce at a rate that results in a stable population, thus leading to low densities. At some point on the reservoir (site 2), the current velocity slows to the point where zooplankton are able to maintain stable populations. This point is termed the zooplankton front, and its position will fluctuate within the reservoir (Marzolf 1990). Further downstream from this point, the nutrients begin to be consumed, or settle into the deeper water, and phytoplankton will suffer losses from sedimentation, grazing, and limited light availability, thus causing the zooplankton density to decrease towards the dam (sites 3 and 4) (Marzolf 1990).

This pattern of distribution in the reservoir could be significant to the paddlefish in that they must seek out areas of locally heavy zooplankton densities. Any extreme concentrations of zooplankton in certain areas of the reservoir could affect the efficiency with which paddlefish encounter the food resources of the reservoir depending upon the distribution of the paddlefish within the reservoir. Because the zooplankton densities are highest in the upper and middle portions of the reservoir, paddlefish will encounter more food resources if they are able to detect and seek these areas.

Zooplankton also can be variably distributed horizontally in a reservoir or lake, especially in openwater or backwater locations. Densities would be expected to be greater in the backwaters of a lake or reservoir, since these areas are less turbulent, less turbid, and often have higher concentrations of nutrients available to the phytoplankton. This study found no significant differences in zooplankton densities among the openwater and backwater stations in the reservoir. The similar densities in the openwater and backwater stations in Livingston Reservoir might be attributed to greater predation losses in the backwaters. Planktivorous fish tend to feed in coves and backwaters due to the greater number of zooplankton in these areas and the availability of cover, which affords protection from predators such as larger fish and birds (Green 1985). Paddlefish have also been shown to feed in quiet, backwater areas (Pitman 1991). Therefore, the smaller than expected numbers of zooplankton in the backwaters could be due to higher rates of predation.

Another reason that the zooplankton might be found in greater than expected numbers in the open water is the tendency of zooplankton to avoid the

shore. Many zooplankton tend to move away from the shore, most likely in order to avoid the high predation pressure in the littoral backwaters (Gliwicz and Rykowska 1992). Even within littoral zones, rotifers tend to move away from the shore and into more open waters, and this "shore avoidance" also has been seen in cladocerans and copepods (Pennak 1989, Preissler 1990, Williamson 1991). In either case, the lower density of zooplankton in the backwaters could force the paddlefish to seek out more feeding areas in the open waters.

Although such behavior might not have much effect upon the adult paddlefish, the younger fish could be hurt by the loss of cover, and subsequent greater predation, experienced by spending more time in open waters. And, as mentioned earlier, any detrimental effect upon young paddlefish will affect the development of a paddlefish population in the reservoir.

Zooplankton also are differentially distributed vertically within the water column. Figure 9 shows that there are slightly more zooplankton in the surface water at night than during the day, although the difference is not significant. If the different types of organisms are taken into account, it is clear that copepods and cladocerans showed a strong tendency to move into the surface waters at night (Figures 9-10). This vertical migration is a very common phenomenon, especially among the copepods and cladocerans, which are stronger swimmers than the rotifers.

The causes of vertical migration are not clear, but several factors probably play an important part in the phenomenon. The most important reason for moving vertically within the water column seems to be predator avoidance, with the organisms moving down during the day in order to avoid planktivorous fish

that feed visually. Dodson (1990) and Gabriel and Thomas (1988) found that predator avoidance was the chief factor in vertical migration among *Daphnia*. Food availability and temperature have also been reported to influence vertical movements in the water column (Dini and Carpenter 1992, Marcogliese and Esch 1992). Vertical migration could be important to paddlefish if they tend to feed at specific positions within the water column, but there is not much known about such behavior.

Paddlefish Bioenergetics Model

In order to estimate the carrying capacity of Livingston Reservoir with respect the paddlefish population, it would be helpful to develop a bioenergetics model that predicts the paddlefish biomass, in terms of density (kg/ha), that can be supported in the reservoir given its present food resources. In order to address the question of suitability of paddlefish food resources, the model must take into account the metabolic requirements of paddlefish and the zooplankton production of the reservoir.

The model I developed is based on Peters' general metabolic rate equation for poikilotherms ($R_{s(p)} = 0.14 W^{0.751}$) (Peters 1983), and its development is illustrated in Appendix C. The general form of the paddlefish bioenergetics model is:

$$k = (EU \times V) / M_p,$$

where k = carrying capacity of the reservoir (kg/ha of paddlefish)

EU = the energy in the zooplankton community utilized by paddlefish

V = volume of the reservoir in which paddlefish feed (L)

M_p = metabolic requirement of paddlefish

The expanded form of the model is:

$$k = \frac{(22 \times 10^6 \cdot [(a \cdot e) + (b \cdot f) + (c \cdot g) + (d \cdot h)] \mu\text{g/yr/L} \cdot i \cdot (100 - j) \cdot m \cdot W \text{ kg/paddlefish} \cdot (V_p + V_s))}{(4.42 \times 10^{14}) \cdot W^{0.751} \mu\text{g/yr/paddlefish} \cdot n}$$

where k = carrying capacity of reservoir (kg/ha paddlefish)

a = biomass of rotifers ($\mu\text{g/L/yr}$)

b = biomass of cladocerans ($\mu\text{g/L/yr}$)

c = biomass of adult copepods ($\mu\text{g/L/yr}$)

d = biomass of copepod nauplii ($\mu\text{g/L/yr}$)

e = efficiency with which paddlefish capture rotifers (%)

f = efficiency with which paddlefish capture cladocerans (%)

g = efficiency with which paddlefish capture adult copepods (%)

h = efficiency with which paddlefish capture copepod nauplii (%)

i = efficiency with which paddlefish encounter zooplankton (%)

j = portion of zooplankton taken by competitive fish species (%)

m = energy utilization efficiency of paddlefish (%)

n = surface area of reservoir (ha)

V_p = volume of reservoir photic zone (L)

V_s = volume of reservoir in addition to photic zone in which paddlefish feed (L)

W = weight of paddlefish (kg)

In order to use this model to estimate the carrying capacity of Livingston Reservoir, I used values from this study to estimate the annual zooplankton production in the reservoir, and estimated values for the other variables. I estimated values for variables a-d (annual biomass of each of the four types of zooplankton measured) by multiplying the average biomass (see Table 5) by the

average number of turnovers per year for each type. The turnovers per year used were 30.9 for rotifers, 19.3 for cladocerans, and 4.5 for copepods, which were taken from a relatively oligotrophic lake in New Hampshire (Makarewicz and Likens 1979). This process resulted in values of 383.8, 111.4, 33.8 and 25.6 $\mu\text{g}/\text{yr}/\text{L}$ for variables a, b, c, and d, respectively.

I used an adult copepod capture efficiency (variable g) of 90.7%, which is an estimate of alewife retention efficiency for a cyclopoid copepod (MacNeill and Brandt 1990). Because of the small size of rotifers and nauplii, I estimated variables e and h to be 15%, and because the cladocerans were larger than the rotifers and nauplii, but smaller than the adult copepods, estimated variable f as 60%. Several studies show that rotifers and copepod nauplii are captured much less efficiently than are adult copepods, and might even be as low as 0% (Rosen and Hales 1981; Burke and Bayne 1986; MacNeill and Brandt 1990), and so the value of 15% used for the efficiency with which paddlefish capture rotifers and copepod nauplii are likely liberal estimates.

There are not many data in the literature that can be used to estimate values for the efficiency with which paddlefish encounter the zooplankton in the reservoir (variable i) or the portion of the zooplankton community that is taken by competitive fish species (variable j). My estimate for variable i was 60%, assuming that the paddlefish would encounter over half of the zooplankton community because of its even distribution among the openwaters and backwaters. However, this efficiency would also be limited by the patchiness of the zooplankton with regards to the four different sites on the reservoir. I estimated that other planktivorous fish in the reservoir (gizzard shad, threadfin

shad, larval fish, etc.) take 75% of the zooplankton community because of the domination of the fish biomass by these other fish (Klussman et al. 1987). I used a value of 15% for the energy utilization efficiency of paddlefish, which is an average of the range of general utilization efficiencies (Odum 1971).

I assumed the photic zone of the reservoir to be between zero and two meters, which is approximately three times the average Secchi depth of 0.63 m, and the resulting value for V_p is 7.2×10^{11} . I estimated a value of 7.92×10^{11} as the additional volume of the reservoir in which paddlefish might feed (V_a), which is the volume from 2 to 4 m, in which zooplankton were found in this study, plus and additional 10% of this volume to take into account the zooplankton below 4 m. The surface area of the reservoir is 36,018 ha, and I used a weight of 6 kg per paddlefish, which was the average weight of the 1986 commercial harvest of paddlefish from Kentucky Lake, Tennessee-Kentucky (Hoffnagle and Timmons 1989).

Using the preceding values, the model predicts that Livingston Reservoir will support a paddlefish density of 1.17 kg/ha. I also predicted other estimates using maximum and minimum best estimates, and predicted a range of possible densities of 0.06 to 7.45 kg/ha.

One important factor that might influence the prediction of the model is the tendency of the cladocerans and copepods to migrate vertically within the water column. In the preceding application of the model, I used zooplankton biomass estimates based on densities during the day. But, data on diel densities from this study indicate that, at certain times during the year, cladocerans and copepods exhibit two- to five-fold increases in density in the surface waters at

night, and could, therefore, increase biomass estimates based on these densities.

Taking such increases into account by increasing the biomass estimates for cladocerans during the summer and winter, and copepods during summer (see Figures 10-11), increases the biomass of paddlefish that the reservoir could support. The range of paddlefish densities that could be supported in the reservoir increased from a range of 0.06-7.45 kg/ha to 0.13-10.45 kg/ha, with a best estimate of only 1.92 kg/ha.

The goals of TPWD state that 62,000 adult and 93,000 juvenile paddlefish are desired in Livingston Reservoir after the stocking program is complete (V. Pitman, Texas Parks and Wildlife Department, personal communication). Depending on the weights of these fish, this translates to a density of about 12 to 24 kg/ha. Therefore, the predictions of the model, even at the top end of the range of densities (9.47 kg/ha), are lower than the desired densities (12-24 kg/ha). Increasing the biomass of the zooplankton due to vertical migration increases the density estimates, but only to a maximum of 10.45 kg/ha, which is still lower than the lowest end of the goal range. Therefore, it seems that Livingston Reservoir will not support a paddlefish population of the size desired, and perhaps one of the chief reasons for this is the size structure of the zooplankton community discussed earlier.

This bioenergetics model is only an educated estimate of the potential paddlefish abundance, and therefore predicts a wide range of paddlefish densities that could possibly be supported by the Livingston Reservoir zooplankton community. Some of the limitations of the model include the inability to accurately estimate variables e-k, which is due to a lack of knowledge of

paddlefish food resources and competitive interactions. But, because even the high end of the range of densities predicted is lower than the low end of TPWD target densities, I recommend that TPWD revise its goals of paddlefish densities in Livingston Reservoir, at least until more research is conducted to better define some of the model parameters.

CONCLUSIONS

The water quality of Livingston Reservoir is sufficient for both a paddlefish population and a zooplankton community upon which paddlefish feed. The range of mean interraker distances in paddlefish was determined to be 0.06-0.08 mm. Measurements of the total length, body length, and width of zooplankton showed that the majority of measurements are greater than the mean interraker distances in paddlefish. But, because the widths of the rotifers and copepod nauplii are close to the interraker distance, and because of the soft-bodied texture of rotifers, paddlefish most likely do not utilize rotifers and nauplii as efficiently as they do the larger cladocerans and copepods.

The zooplankton community of Livingston Reservoir comprises zooplankton taxa similar to those found in other reservoirs and lakes in Texas and the United States. The mean annual standing crop of zooplankton in Livingston Reservoir is 173 org/L, which is greater than that found in other Texas reservoirs. The community is dominated in terms of density and biomass by rotifers and copepod nauplii, and even the cladoceran and copepod populations are made up of small members of these groups. Such a size structure, which might be the result of heavy predation by planktivorous fish, could limit the amount of paddlefish Livingston Reservoir is able to support. The lack of larger zooplankton also could have serious effects upon the growth and survival of the young paddlefish that depend upon them.

The zooplankton community of the reservoir is distributed horizontally in greater densities toward the middle of the reservoir, in the transition zone between the riverine and lacustrine zones (Soballe et al. 1992). Zooplankton are

found in similar densities in the openwaters and backwaters. The copepods and cladocerans show strong vertical migration within the water column, a situation that also could be significant to the feeding habits of the paddlefish.

Although the use of the paddlefish bioenergetics model developed in this study could help determine the overall suitability of the Livingston Reservoir zooplankton community as a food resource for a paddlefish population, the model is presently limited by the lack of knowledge of paddlefish foraging, food resource dynamics, and resource competition among planktivores. Because of the domination of the density and biomass by the small rotifers and copepod nauplii, which paddlefish utilize less efficiently than larger copepods and cladocerans, and the domination of the cladoceran and copepod communities by smaller organisms, the present zooplankton community of Livingston Reservoir will most likely not be sufficient to support a paddlefish population of the desired target size.

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APPENDICES

Appendix A. Physiochemical field measurements from Livingston Reservoir, Texas (March 1992 - March 1993).

<u>Date</u>	<u>Temp. (°C)^a</u>	<u>DO (mg/L)^b</u>	<u>Trans (m)^c</u>	<u>pH</u>	<u>Conduct (μS/cm)^d</u>	<u>Depth (m)^e</u>
March 26 1992	17.8	7.4	0.27	7.66	249.2	18.67
April 8	19.0	7.6	0.30	7.82	290.7	20.25
April 22	21.0	7.2	0.33	7.90	275.5	6.08
May 19	20.6	6.7	0.47	7.98	456.9	21.13
June 5	23.2	7.9	0.32	8.5	314.4	20.38
June 19	27.8	7.8	0.46	8.3	368.8	23.58
July 1	27.2	7.1	0.46	8.4	412.8	17.50
July 22	28.0	6.8	0.55	8.5	469.9	21.08
August 11	30.0	6.4	1.30	7.7	487.5	20.21
August 25	28.1	6.4	1.13	8.4	342.0	25.25
September 3	27.6	6.8	0.94	8.1	297.3	22.50
September 20	28.6	6.6	1.20	8.2	322.8	20.58
October 27	23.4	9.8	1.18	8.3	454.8	19.63

Appendix A. Continued.

<u>Date</u>	<u>Temp. (°C)^a</u>	<u>DQ (mg/L)^b</u>	<u>Trans (m)^c</u>	<u>pH</u>	<u>Conduct (μS/cm)^d</u>	<u>Depth (m)^e</u>
November 18	16.7	8.8	1.03	8.0	490.2	20.00
December 15	11.1	10.5	0.65	8.0	573.2	22.46
January 13 1993	10.3	9.2	0.26	7.5	276.9	20.83
February 19	11.4	10.1	0.26	7.8	245.2	21.67
March 8	14.1	8.5	0.24	7.8	274.4	20.38
TOTAL	20.8	7.4	0.63	8.0	362.3	20.79

^a Water temperature measured in degrees Centigrade

^b Dissolved oxygen

^c Transparency

^d Conductivity measured in microsiemens/cm

^e Mean water depth at all sites and stations combined

Appendix B. Physiochemical lab measurements for Livingston Reservoir, Texas (March 1992 - March 1993).

<u>Date</u>	<u>Turbidity (FTU)^a</u>	<u>Alk (mg/L)^b</u>	<u>Hard (mg/L)^c</u>	<u>Cl^d</u>	<u>NO₃^d</u>	<u>NO₂^d</u>	<u>NH₄^d</u>	<u>PO₄^d</u>
March 26 1992	-	-	256.0	-	-	-	-	-
April 8	-	-	-	-	-	-	-	-
April 22	56.8	84.2	97.0	13.225	1.150	0.046	0.801	0.066
May 19	47.0	94.6	129.1	13.900	0.613	0.001	0.353	0.411
June 5	34.3	84.4	120.1	13.157	0.175	0.000	0.056	0.159
June 19	39.5	78.1	108.9	1.488	0.375	0.000	0.338	0.068
July 1	33.0	94.4	128.6	17.775	0.563	0.003	0.344	0.103
July 22	26.5	92.0	118.0	24.500	0.350	0.016	0.280	0.084
August 11	26.9	97.8	122.3	24.500	1.150	0.024	0.330	0.218
August 25	34.4	102.6	122.3	3.325	0.563	0.031	0.343	0.145
September 3	43.4	82.6	130.0	24.500	-	0.056	0.204	0.343
September 20	27.4	96.8	132.5	20.050	1.013	0.058	0.248	0.236
October 27	34.8	101.4	134.5	13.975	1.313	0.026	0.278	0.300

Appendix B. Continued.

Date	<u>Turbidity (FTU)^a</u>	<u>Alk (mg/L)^b</u>	<u>Hard (mg/L)^c</u>	<u>Cl^d</u>	<u>NO₃^d</u>	<u>NO₂^d</u>	<u>NH₄^d</u>	<u>PO₄^d</u>
November 18	35.0	85.1	132.6	16.313	1.625	0.017	0.398	0.304
December 15	53.6	78.8	110.9	17.000	0.788	0.012	0.481	0.346
January 13 1993	65.0	51.9	83.8	22.700	0.788	0.002	0.815	0.195
February 19	74.4	77.8	110.9	22.150	0.925	0.009	0.663	0.134
March 8	79.5	80.3	107.4	16.225	0.725	0.006	1.109	0.111
TOTAL	44.5	85.7	119.1	16.640	0.757	0.018	0.439	0.199

^a Measured in formazin turbidity units (1 FTU = 1 nephelometric turbidity unit)^b Total alkalinity measured as mg/L as CaCO₃^c Water hardness measured as mg/L as CaCO₃^d Measured as mg/L

Appendix C. Development of paddlefish bioenergetics model.

The basic form of the paddlefish bioenergetics model is $k = EU * V / M_p$, where k is the carrying capacity of the lake or reservoir for paddlefish, EU is the energy in the reservoir utilized by paddlefish, V is the volume of the reservoir, and M_p is the metabolic requirement of paddlefish.

1) EU (energy utilized)

Rotifers : a (μg dry mass) * e (efficiency of capture) +

Cladocerans : b (μg dry mass) * f (efficiency of capture) +

Adult copepods: c (μg dry mass) * g (efficiency of capture) +

Nauplii: d (μg dry mass) * h (efficiency of capture) =

$$[(a * e) + (b * f) + (c * g) + (d * h)] * i * (100 - j) \mu\text{g/yr/L},$$

where i = efficiency with which paddlefish encounter zooplankton, and j =
portion of zooplankton taken by competitive fish species

2) M_p (metabolic requirements of paddlefish)

Standard metabolic rate for poikilotherms: $R(\text{Watts}) = 0.14 * W^{0.751}$

1 Watt = 1 Joule/s

$22 \times 10^6 \text{ J} = 1 \text{ kg dry mass}$

so, the metabolic requirement of paddlefish (M_p) in μg dry mass/yr/paddlefish:

$$M_p = \frac{0.14 * W^{0.751} \text{ watts/paddlefish} * 1 \text{ J/s/watt} * 1000 \text{ g/kg} * 1,000,000 \mu\text{g/g} * 31,536,000 \text{ s/yr}}{22 \times 10^6 \text{ J/kg} * m}$$

where m = efficiency with which paddlefish transfer available energy (J) into

kg of dry mass, and W = weight of paddlefish in kg

$$= (W^{0.751} * 4.42 \times 10^{15}) / (22 \times 10^6 * m)$$

- 3) The volume of the reservoir in which paddlefish feed is determined by adding
adding the volume of the photic zone (V_p) to the addition volume of the
reservoir in which paddlefish feed (V_e). Therefore, the volume of the reservoir

Appendix C. Continued

in which paddlefish feed is:

$$V = V_p + V_s$$

4) Therefore, filling the above terms into the general model leads to:

$$k = \frac{22 \times 10^6 \cdot [(a \cdot e) + (b \cdot f) + (c \cdot g) + (d \cdot h)] \mu\text{g/yr/L} \cdot i \cdot (100 - j) \cdot m \cdot (V_p + V_s)}{4.42 \times 10^{16} \cdot W^{0.761} \mu\text{g/yr/paddlefish}}$$

5) The units of k, from step 4, are paddlefish. In order to transform k into paddlefish density in kg/ha, k from step 4 must be multiplied by W and divided by the surface area of the reservoir in hectares (n). Solving the equation for k, in kg/ha, leads to:

$$k = \frac{(22 \times 10^6) \cdot [(a \cdot e) + (b \cdot f) + (c \cdot g) + (d \cdot h)] \mu\text{g/yr/L} \cdot i \cdot (100 - j) \cdot m \cdot W \text{ kg/paddlefish} \cdot (V_p + V_s)}{(4.42 \times 10^{16}) \cdot W^{0.761} \mu\text{g/yr/paddlefish} \cdot n}$$

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